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A MANUAL

OF

DENTAL ANATOMY

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DENTAL ANATOMY

HUMAN AND COMPARATIVE

BY

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PREFACE TO THE THIRD EDITION.

In the following pages it has been my endeavour to give an outline of the more important facts of Odontology, such as may serve for an introduction to a more extended study of the subject. Within the limitations of an elementary text-book, more than this seems not to be practicable, and I have therefore omitted, or passed by with brief mention, hypotheses as to the genesis of teeth and the like, which, however interesting, have not as yet so established themselves as to meet with general acceptance.

In a book of this kind it is neither desirable to burden the text with many references, nor to omit them altogether; the rule which I have followed, I fear by no means always consistently, has been to give references only to works and papers which might be regarded as in a measure classical, and to those which, by reason of being somewhat new, have not yet found their way into systematic treatises.

But I must take this opportunity of expressing my obligation to the Odontographies of Prof. Owen and of Giebel, to Prof. Flower's Lectures on Odontology, his articles in the Encyclopædia Britannica, and his many other papers; to the article on Teeth by Dr. Worthman in the "American System of Dental Surgery," and to the rich contributions of Prof. Cope and Prof. Marsh to our knowledge of the varied extinct mammalian fauna of America, of all of which I have made free use.

CHARLES S. TOMES.

37, Cavendish Square,
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A

MANUAL OF DENTAL ANATOMY

HUMAN AND COMPARATIVE.

CHAPTER I.

THE TEETH OF MAN.

THE range of the subject of Dental Anatomy turns upon the meaning which is attached to the word "Tooth;" but, although this chapter might most appropriately open with a definition of this word, it is very much easier to explain what is ordinarily understood by it, than to frame any single sentence which shall fulfil the requirements of logical definition. Most vertebrate and a great many invertebrate animals have certain hard masses in or near to the orifice of the alimentary canal, *i.e.*, the mouth; by these hard masses, sometimes of bony and sometimes of horny nature, various offices in connection with the prehension or comminution of food are performed, and to them the term "teeth" is applied. But whilst in some animals these functions are performed by horny bodies, recent researches have shown that at all events in several cases, these horny teeth are superimposed upon true tooth germs, calcified to some extent, which they supersede; the exact relation of the one to the other requires further elucidation. In

many animals teeth have come to be used for purposes other than those of nutrition, such as for sexual warfare; but it can hardly be doubted that teeth had primarily to do with the nourishment of their possessor.

The subject of the homologies of the teeth cannot be fully entered upon until the details of their development have been mastered; still a few words may even at the outset be devoted to the elucidation of their real nature.

The mucous membrane which lines the alimentary canal is continuous with—is, indeed, a part of—the external skin, with which it blends at the lips. Now if a young dog-fish, just about to be hatched, be examined, it will be found that it has no distinct under lip, but that its skin turns in over its rounded jaw without interruption. The skin outside carries spines (placoid scales),(1) and these spines are continued over that part of it which enters the mouth and bends over the jaws; only they are a little larger in this latter position. If the growth of the dog-fish be followed, these spines of the skin which cover the jaws become developed to a far greater size than those outside, and the identity and continuity of the two become to some extent masked. No one can doubt, whether from the comparison of adult forms or from a study of the development of the parts, that the teeth of the shark correspond to the teeth of other fish, and these again to those of reptiles and mammals; it may be clearly demonstrated that the teeth of the shark are nothing more than highly developed spines of the skin, and therefore we infer that all teeth bear a similar relation to the skin. This is what is meant when teeth are called "dermal appendages," and are said to be perfectly distinct from the internal bony skeleton of the animal; the teeth of the shark (and of many other creatures) are not only deve-

(1) "The placoid scale has the structure of dentine; is covered by enamel, and is continued at its base into a plate formed of osseous tissue." Gegenbaur's Comparative Anatomy, translated by F. Jeffery Bell, p. 424.

loped in but always remain imbedded in tough mucous membrane, and never acquire any connection with the bone. Indeed, all teeth alike are developed from a part of the mucous membrane, and any connection which they may ultimately get with the bone is a secondary matter. As it has been well expressed by Dr. Harrison Allen ('Anatomy of the Facial Region'), "if the hairs of the scalp were to be inserted into the skull, or of the moustache into the upper jaw, we should express great astonishment, yet such an extreme proposition is no more remarkable than what is seen to take place in the jaws," again "the feathers of certain birds making impressions on the radius, the whalebone pendent from the roof of the mouth, are examples of this same association of tegumentary appendages with the bones."

To these may be added the horny plates of Ornithorhyncus, which are pure hardenings of the stratum corneum of the oral epithelium, but which have definite beds provided for them on the bones.

In their simpler forms, then, teeth are met with as very numerous spines, differing but little from the spines of the skin except in size, and still less from one another. In many fish the teeth, though more specialised, are scattered over almost every one of the numerous bones which form part of the walls of the mouth and pharynx; in reptiles they are much more limited in position, and in mammals are absolutely confined to the intermaxillary, maxillary, and mandibular (lower maxillary) bones. In fish and reptiles it is the exception for the teeth in different parts of the mouth to differ markedly from each other; in mammals it is the rule.

Teeth owe their hardness to an impregnation with salts of lime; the organic matrix may be of albuminoid character, in which case the tooth is of horny consistence, and is spoken of as "cornified;" or the matrix may be, like that of bone,

gelatigenous, in which case the tooth is much more richly impregnated with salts, and is spoken of as "calcified."

Horny teeth, so far as they have been investigated, consist of aggregations of cells of the stratum corneum of the oral epithelium, and they are penetrated on their under side by the papillæ whose enormously exaggerated epithelial coats have built them up.

The great mass of a calcified tooth is usually made up of "dentine," which gives to it its characteristic form, and often practically constitutes the whole tooth: to this may or may not be added enamel and cementum.

Without further prelude we may pass to a description of the human teeth, this course appearing to me, after some little consideration, to afford to the student the most advantageous introduction to the subject, as he must necessarily already possess some knowledge of their forms, while to the matters alluded to in the preceding pages more full reference will be made hereafter.

In the human subject no tooth rises above the level of its fellows, and the teeth are arranged in close contact, with no interspaces between them. The teeth are ranged around the margins of the jaws in a parabolic curve, or something approximating to one; in the lower races of mankind the curve tends to a squarish, oblong form, owing to the prominence of the canines (compare the figure of the dentition of Simia satyrus), whilst a deviation in the opposite direction is daily becoming more common in the most highly civilised races, resulting in a contour to which in extreme cases the name of V-shaped maxilla is applied.

It may be stated, as generally true, that the teeth are somewhat larger on their labial than on their lingual aspect, a result which necessarily follows from their standing without interspaces along a curved line. And as great variations in size and shape, as well as in colour, are found to exist between different individuals, it is only possible to give

such a description as shall apply to the generality of teeth.

The teeth of the upper jaw are ranged along a curve of larger dimensions than those of the lower, the incisors passing in front of the corresponding lower teeth, and the external cusps of the bicuspids and molars closing outside those of the lower teeth.

There are, however, some points of detail to be noted in the relation borne by the upper to the lower teeth, besides that comprised in the general statement that the former lie outside the latter, by which it is brought about that each tooth is antagonised by portions of two teeth in the other jaw, instead of having only a single opponent.

The upper incisors and canines, when the mouth is closed, from the larger size of the arch in which they are arranged, shut over and in front of the lower teeth, concealing the upper thirds of their crowns; while the external tubercles of the bicuspids and molars of the lower jaw are received into the depressions between the external and internal tubercles of the similar teeth in the upper jaw, thus allowing the external tubercles of the upper teeth to close externally to the outer tubercles of the lower row.

From this arrangement of the tubercles, we are enabled in mastication to use the whole surface of the crowns of the opposing teeth; the act of mastication being performed by bringing the external tubercles of the under molars opposite to those of the upper row; whence, by the lateral motion of the under jaw inwards, their external tubercles pass down the inclined surfaces of the external, and up those of the internal tubercles of the upper teeth, crushing in this action any interposed substance.

It will also be observed that, from the difference of width in the incisors of the two jaws, the central incisors of the upper extend over the centrals and half of the laterals of the under row, and that the superior laterals lie over the

remaining half of the inferior laterals and the anterior half of the canines of the lower jaw. The canines close over the halves of the canines and first bicuspids, while the first bicuspids impinge on the half of the first and half of the second bicuspids of the lower row. The second upper bicuspids close upon the anterior third of the opposing first molars and the posterior half of the second bicuspids.

The first molars oppose the posterior two-thirds of the first, and one third of the second molars of the lower jaw, while the second upper molars close upon the unoccupied posterior third of the second and the anterior third of the wisdom teeth. The wisdom tooth of the upper being smaller in size than that of the lower jaw is perfectly opposed by that portion of the latter left unoccupied by the second under molar tooth.

By this admirable arrangement no two teeth oppose each other only, but each tooth in closure of the jaw impinges upon two, so that should a tooth be lost, or even two alternate teeth, still the corresponding teeth of the opposite jaw are to some extent opposed, and thus remain useful. For when a tooth is wholly unopposed, a process is apt to be set up in the jaw by which the useless organ is gradually ejected. The direction of the teeth in the upper is vertically downwards and slightly forwards, while those of the lower jaw are placed vertically, the molars tending slightly inwards.

It is usual to represent the dentition of any animal by what is termed a dental formula, which enables the reader at a glance to see the number of teeth of each variety possessed by the creature. Thus, instead of writing out at length that man has two incisors on each side in both upper and lower jaws, one canine, two bicuspids or premolars, &c., it is written thus :—

$$\text{i. } \frac{2}{2} \text{ c. } \frac{1}{1} \text{ pm. } \frac{2}{2} \text{ m. } \frac{3}{3} = 32 :$$

or in the deciduous set:—

$$\text{i. } \frac{2}{2} \text{ c. } \frac{1}{1} \text{ m. } \frac{2}{2} = 20.$$

For the purpose of description three parts of the tooth are distinguished by name, viz., the crown, neck, and root.

This distinction of parts which we make in describing human teeth, when we speak of crown, neck, and root, is applicable to the great majority of mammalian teeth, though there are some few simple forms of teeth in which no such differentiation of parts can be seen.

The crown is that portion which is exposed above the borders of the gum, and is in human teeth coated with enamel; the neck is that portion which corresponds to the edge of the gum, and intervenes between the edges of the bony sockets and the edge of the enamel; the root is that part which is enclosed within the bony socket, and is covered by cementum.

Of these it is to be remarked that the "neck," although a convenient and necessary term for descriptive purposes, marks an arbitrary division of less importance than that expressed by crown and root; also that although this division into three parts can be made in the case of socketed teeth of limited growth, no such distinction of parts can be made in teeth of perpetual growth.

Special names have been applied to the various surfaces of the crowns, as, owing to the curvature of the alveolar border, terms which had reference to front, back, or sides would, in different parts of the mouth, indicate different surfaces, and so lead to confusion.

The lips and tongue and the median line of the mouth, however, are not open to this objection, so the surfaces which are directed outwards towards the lips are called "labial;" and those inwards towards the tongue "lingual;" the interstitial surfaces are called "median" and "distal,"

the word median being applied to the surface which would look towards the middle line of the mouth had the alveolar border been straightened out. In other words behind the canine, the "median" is equivalent to anterior, and "distal" to posterior surface.

Forms of the several Teeth.—It is usual to speak of the teeth as being modified cones, and to attribute their variations to deviations from this typical shape. In a broad sense this may be true of the simplest teeth, such as are met with in some fish and reptiles and monophyodont mammals, which are little more than simple cones; but there are indications which would point to something more complex than this as a very early form of mammalian tooth, for even among the monophyodonts, as I have elsewhere pointed out, the armadillo has a bilobed tooth germ, the one cusp predominating over the other. And the teeth of the Ornithorhyncus, which from many considerations must be regarded as exceedingly early forms of mammalian teeth, were broad topped, had on one side somewhat pronounced cusps, and on the other a crenulated margin, and had several short roots. In Mesozoic times most mammals had the full typical number of teeth, the molars were usually tuberculated, and in many groups a very distinct series of modifications from parent forms has been traced out. Proceeding from these generalised forms the specialisation usually takes the form of a shortening of the length of the jaws, accompanied by a reduction in the number of the teeth, some teeth being suppressed and others taking on some particular development. This specialisation of teeth frequently goes on hand-in-hand with specialisation of limbs.

It has been usual to suppose that the teeth which are missing in man are the third incisor on each side and the first and second premolars, but reasons have been advanced which throw doubt upon this conclusion as regards the incisors (Albrecht, *Zoolog. Anzeig.*, 1879; Prof. Sir W. Turner, *Journal*

of Anatomy and Physiology, 1885 ; A. Wilson, *British Dental Association Journal*, April, 1885 ; Edwards, *British Dental Association Journal*, December, 1885). From the study of cases of cleft palate it has been found that it is not at all certain that the cleft usually runs along the site of the suture between the intermaxillary bones and the maxilla, for it often appears to be well within the limits of the intermaxillary bone, and so lends some support to the idea of Albrecht that there are two intermaxillary bones on each side, and that the cleft runs along the division between them. And it is far from uncommon for a tooth of incisor type to lie beyond the cleft and close against the front of the canine ; to this tooth Sir W. Turner, pending decision as to its homologies, gives the name of precanine. The argument put briefly is this ; a tooth outside the cleft and close to the canine is so common of occurrence that its position there must be due to something other than accident, the normal number of incisors not being exceeded. But there is a case on record in which this precanine existed although there were four incisors upon the intermaxillary portion, which was isolated by a double cleft ; in this specimen therefore the precanine was evidently i^3 of the normal mammalian dentition, and it is therefore not unlikely that it is always so ; if this inference be correct, then the lost incisor in man is probably i^2.

I do not think that we have at present the data upon which to certainly determine the fundamental form of the mammalian tooth, but there is evidence that all the teeth in the jaw of a mammal may have been derived from a common form ; in other words, marked though the distinction between incisors, canines, bicuspids, and molars seems to be at first sight, a closer inspection reveals various gradational or transitional characters linking them together, though there are gaps in the chain not bridged over by forms known to us. This may be seen by a careful study of the human teeth, as I

shall endeavour to show; but it is much more conspicuously seen in an extinct animal (Homalodontotherium, an extinct ungulate from Patagonia, described by Professor Flower, Philos. Trans. 1874), which apparently possessed the full typical number of mammalian teeth, viz., forty-four. The point in which its dentition is chiefly instructive is that the teeth, in close juxtaposition one with another, present an exceedingly perfect gradation of form from the front to the back of the mouth, no tooth differing markedly from its neighbour, though the difference between, say, the first incisor and first molar, is exceedingly great. In Professor Flower's words, "it is only by the analogy of other forms that they can be separated into the groups convenient for descriptive purposes, designated as incisors, canines, premolars, and molars."

In viewing the gradational characters which do exist between the various human teeth, it must not be forgotten that some links in the chain have dropped out and are absent. Mention has already been made of the full typical number of mammalian teeth being 44, *i.e.*

$$\text{i. } \frac{3}{3} \text{ c. } \frac{1}{1} \text{ prm. } \frac{4}{4} \text{ m. } \frac{3}{3} = 44$$

Incisors.—Of these there are four in each jaw; two central, two lateral incisors. Their working surfaces form wedges, or obtuse and blunt-edged chisels, calculated to divide food of moderate consistency.

Upper Incisors.—The centrals are very much larger than the laterals, and viewed either from the back or front taper with some regularity from the cutting edge to the point of the root, the neck not being marked by strong constriction. The crown of the tooth, as seen from the front, is squarish, or more strictly, oblong, its length being greater than its breadth.

The median side, by which it is in contact with its fellow,

is a little longer than the distal, so that the median angle of the crown is a little lower, and, as a necessary consequence, a little more acute than the distal angle of the cutting edge. Near to their base the crowns narrow rather abruptly, so

FIG. 1 ([1]).

that at the neck a space is left between the contiguous teeth.

The labial surface is slightly convex in each direction, and often presents slight longitudinal depressions, which end at the cutting edge in slight notches.

In recently-cut teeth the thin cutting edge is elevated into three slight cusps, which soon wear down and disappear after the tooth has been in use.

The edge of an incisor may be regarded as formed by the bevelling off of the dentine of the lingual surface, which is nearly flat from side to side, with a slight tendency to concavity, while from above downwards it is distinctly concave, and often presents longitudinal depressions similar to those on the labial surface. The lingual surface towards the gum terminates in a distinct prominence, oftentimes amounting to a bounding ring of enamel, termed the *basal ridge*, or, in the language of comparative anatomy, the *cingulum*. It is variable in the extent of its development; it rarely rises

([1]) Front and side view of a left upper central incisor.
a Distal surface. *b* Neck. *c* Root.

into a central prominence at the back, but in the angle where the ridges of the two sides meet a deep pit is often left in the enamel, which is a favourite site for caries. The crown, or what amounts to the same thing, the enamel, terminates on the lingual and labial aspect of the tooth in a curved line, the convexity of the curve being directed upwards towards the gum; on the interstitial surfaces, both median and distal, the curve is less regular, and its contour would be more correctly described as V-shaped, the apex of the V being towards the crown of the tooth and away from the gum. The dentist will do well to remember the disposition of the enamel in this situation, as it is a point of some importance in shaping the cervical edge of a cavity preparatory to filling it.

The transverse indentations of the enamel met with both on lingual and labial surfaces, though more especially in the latter, are marks of arrest of development, and, common as they are, are to be regarded as abnormalities.

The central incisors are larger than the laterals, though not in so great degree as is the case in the anthropoid apes.

The pulp cavity bears a general resemblance to the external contour of the tooth; towards the cutting edge it is very thin, and is prolonged at its two corners to a slight extent into "cornua;" at the neck it is cylindrical, and is also cylindrical in the root, tapering gradually till it approaches close to the apex, when it becomes suddenly constricted.

Upper lateral incisors are in every dimension somewhat smaller than the centrals. They widen somewhat abruptly near to the cutting edge, but below this they taper pretty regularly to the end of the root; the labial surface is convex in each direction, while the lingual surface is perhaps rather flatter than that of a central incisor.

The outer (distal) angle of the crown is far more rounded

or sloped away than in the centrals, and the distal surface, looking towards the canine, is in a slight degree convex; the median surface may be slightly concave.

Fig. 2 (1).

The enamel terminates towards the gum in contours precisely similar to those which obtain in the centrals: but the basal ridge, or cingulum, is often more strongly pronounced, and the presence of a central tubercle upon it is less infrequent. From this greater prominence of the cingulum and consequent more marked depression in front of it, caries is more frequent upon the lingual surfaces of upper lateral than upon those of upper central incisors.

The pulp cavity is, relatively to the whole tooth, perhaps a little larger than in the central incisors; in other respects the same description will suffice.

Lower central incisors are very much narrower than those of the upper jaw; not more than half the width at their cutting edges, which again are much wider than the necks of the teeth.

From before backwards they are deep at the neck; hence the fangs are very much flattened from side to side, and rotation is inadmissible in the attempt to extract them.

The enamel contour at the neck is similar to that of the upper incisors, but there is no well-marked cingulum.

Lower lateral incisors are, unlike the upper teeth, distinctly larger than the centrals in each one of their dimen-

(1) Front and side view of a left upper lateral incisor.

sions, but more especially in the length of their fangs, which are much flattened, and often present on their sides a median longitudinal depression, sometimes amounting to an actual groove.

Fig. 3 (1).

The distal angle of the crown is rounded off like that of the upper lateral incisors, though not so markedly.

Canines, Cuspidati, Eye Teeth, are, in all respects, stouter teeth than the incisors ; not only are the crowns thicker and stronger, but the roots are very much longer.

The crown terminates in a blunt point, which lies in a straight line with the long axis of the root; a feebly pronounced line or ridge runs down the outer surface of the tooth from this point to the neck. The crown slopes away both before and behind the point or cusp, but as that side of the tooth which lies next to the bicuspid is convex, and as it were produced towards that tooth, the slope is longer on the distal than on the mesial half of the crown. The crown thus not being perfectly symmetrical renders it easy to determine at a glance to which side of the mouth the canine belongs.

The internal or lingual surface is not concave like that of the incisors, but is in a slight degree convex, and a median ridge runs down it from the apex of the cusp ; this ridge where it meets with the ridge which borders the lingual surface and corresponds with the cingulum of the incisor

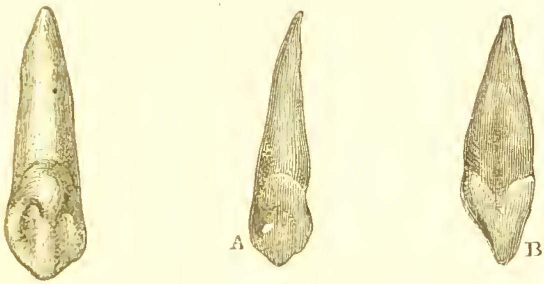
(1) Front and side view of lower central incisor.

teeth, is often developed into a well-marked prominence or cusp.

In transverse section the neck is nearly triangular, the outer or labial being much wider than the lingual aspect.

Lower canines are less pronounced in form than the corresponding upper teeth: the point is more blunted, the fang shorter, the perpendicular labial ridge not being traceable, and the want of symmetry between the mesial and distal halves of the crown less marked. The lingual surface has perhaps a greater tendency to concavity.

Fig. 4 (1).



Premolars, Bicuspids, are eight in number, two on each side of both upper and lower jaws, and they correspond to the third and fourth premolars of the typical mammalian dentition, the first and second premolars not being represented in man (2).

Upper Premolars.—The crown, as seen looking upon its grinding surface, is roughly quadrilateral, its outer or labial border being, however, larger and thicker than its inner, and the teeth are carried round the curve of the alveolar border mainly by means of this difference in size in the external and internal portions of the canines and the two bicuspids.

(1) Lingual, labial, and distal surfaces of an upper canine, showing the basal cusp and the three ridges which converge towards it.

(2) Mr. A. Wilson holds that prm^1 and prm^1 have disappeared.

As is implied by its name, the crown has two cusps, of which the outer is the larger and stouter, and broader. The outer and inner surfaces (labial and lingual) are convex and smooth, with no basal ridges at the edge of the gums. The inner and outer cusps are not joined by a transverse

Fig. 5 (1).

ridge; instead of this there is a deep transverse (concave towards labial side) fissure; in point of fact the cingulum has been elevated to form the inner cusp, and forms slight elevations bordering the anterior and posterior (median and distal) edges of the grinding surface. The median surface, where it fits against the canine, is concave.

The root is single, and much compressed from side to side: very often, however, it is double for the greater part of its length, and if not so divided is often marked by a groove upon each side indicating a tendency towards such division. The outer border of the root is also often marked by a longitudinal furrow, which may amount to complete division. In fact a bicuspid may have three perfectly distinct roots, like a molar, and like the premolars of monkeys, in which three is the normal number of roots. The first bicuspid is more variable in respect of its roots than the second.

The second upper bicuspid differs from the first in that the difference in size between its outer and inner cusps is less, the inner cusp being relatively considerably larger, and, indeed, often preponderating over the labial cusp in length, so that the labial and lingual surfaces are nearly equal.

(1) Grinding surface of an upper bicuspid.

The pulp cavity in the crown is furnished with distinct cornua; at the neck it is very much flattened from side to side, being often reduced to a mere fissure, which is however considerably larger at its two extremities than in its middle. Hence the pulp cavity of an upper bicuspid is difficult to fill; a difficulty again increased by the impossibility of always discovering what number of fangs it has, as their division sometimes takes place rather high up.

Lower premolars are smaller teeth than those of the upper jaw, and are quite distinct in shape. The outer or labial cusp is bent inwards, and the labial surface of the crown is very convex. The inner cusp is but feebly developed, and is connected with the outer by a low ridge; it is also narrow.

The root is rounded, a little larger on its outer side than on its inner, and tapers regularly towards its point; the pulp cavity is cylindrical at the neck, and also tapers regularly in the root. The cornu of the pulp which corresponds to the inner cusp is but feebly developed.

The second lower bicuspid differs a good deal from the first; its crown is much squarer and larger in all its dimensions. The inner cusp reaches to a higher level and is stouter, and the greater development of the ridge which bounds the posterior (distal) border of the grinding surface makes it attain to such a large size as to make the tendency towards a transition from the bicuspid type to the quadricuspid type of a true molar very evident. It is rare for any tendency for a division into two roots to be met with; when it does occur it bears a curious similarity to the form of root met with in the anthropoid apes (cf. the chapter relating to the teeth of monkeys).

The differences between a well-marked incisor, canine, or premolar are so strongly pronounced that the resemblances which underlie them are apt to be overlooked.

Nevertheless a very distinct gradation may be traced, and

it is far from uncommon to meet with teeth which possess in a marked degree transitional characters. If the external or distal angle of a lateral incisor be sloped off more than usual, while at the same time its cingulum and basal prominence be well marked, it makes no bad imitation of a diminutive canine; and such laterals are often to be met with by any who search for such deviations from the normal form.

FIG. 6 ([1]).

Thus the form characteristic of a lateral incisor, if it be a little exaggerated, very nearly gives us the form of a canine, and if we look at the teeth of an Orang the lateral incisor is to all intents a diminutive canine; and in the present discussion the great comparative size of the canine, which is traceable to readily intelligible causes, may be put aside, as it tends to obscure the point to be here insisted on.

Between the canines and the bicuspids a similar relationship in form exists, and it is more apparent in the lower than in the upper jaw. The fact that at the base of the inner or lingual aspect of the canine is to be found an elevation of the cingulum, in many instances amounting to a low cusp, has been already noted; and it has already been pointed out that the inner cusp of the first lower bicuspid is both smaller and lower than the outer. A longitudinal section through the crowns of the two teeth will demon-

([1]) Lower first bicuspid, seen from the inner side, and showing the preponderance of its outer over its inner cusp.

strate without the necessity of further description that the basal cusp of the canine and the inner cusp of the bicuspid are the same thing, differing only in degree, while it is interesting to note that the pulp chamber in the bicuspid has hardly any prolongation towards the small inner cusp, so that the resemblance between the two teeth is thus made more complete.

This close relationship of canines and bicuspids will be

Fig. 7 [1].

again considered in the chapter on the Homologies of the Teeth; for our present purpose it will suffice to merely point out its existence. The transition from the bicuspids to the molars is more abrupt; at least it is not so easy to point out exactly how a modification of the one would arrive at the form of the other. But it merely needs an exaggeration of the differences existing between a canine and a first bicuspid to make a good imitation of a second bicuspid.

If any one will take the trouble to make mental note of the deviation in form which he meets with in teeth, he will find that they almost invariably consist of approaches towards the form of the teeth on either side of them; and will infallibly be led to the conclusion that incisors, canines, and bicuspids are not three patterns of teeth perfectly

[1] Section of a lower canine and first bicuspid, showing the characters common to the two.

distinct, and each *sui generis*, but that they are modifications of one and the same pattern. I may add, that comparative odontology teaches us the same thing, and demonstrates clearly the substantial identity of the three forms, as also of the true molars.

Upper molar teeth have crowns of squarish form, the angles being much rounded off. It may be premised that the first molar is more constant in shape than the second, and this latter than the third; with this proviso the first and second may be described together.

The masticating surface carries four subequal cusps, two labial or external and two lingual or internal; the anterior internal cusp is distinctly the largest, and it is connected with the posterior external cusp by a thick oblique ridge of enamel, the remaining two cusps having no such connection.

This oblique ridge on the upper molars is met with in man, the anthropoid apes, and certain New World monkeys.

The grooves which separate the cusps pass down on to the labial and lingual surfaces of the crown, but are lost

Fig. 8 (1).

before reaching the gum; where they terminate, however, there is often a pit, which is a very favourite situation for caries, especially on the labial aspect of the teeth. It is very rare to see the grooves passing down upon the mesial or distal surfaces of the crown, a raised border of enamel generally cutting them short in this direction.

(1) Masticating surface of a first upper molar of the left side; the oblique ridge connects the anterior internal with the posterior external cusp.

The roots are three in number, two external or labial, and one internal or palatal. The latter is the largest, and runs in a direction more strongly divergent from the axis of the crown than the other roots. It is directed obliquely inwards towards the roof of the palate, is subcylindrical, and often curved.

The external roots are less cylindrical, being mutually compressed, so that their largest diameter is transverse to the dental arch ; the anterior is rather the larger of the two, and is more strongly pronounced on the side of the neck of the tooth. The anterior labial root is occasionally confluent with the palatine root, but still more frequently the posterior labial and palatine roots are confluent : occasionally, also, four distinct roots may be met with.

Third molars, *dentes sapientiæ*, wisdom teeth, of the upper jaw, resemble in a general way the first and second molars ; that is, when they are well developed and placed in a roomy dental arch. But amongst more civilised races it may almost be said to be exceptional for the wisdom teeth to be regular either in form or position, so that extreme variability prevails among these teeth.

The two inner tubercles are often blended together and the roots confluent, forming an abruptly tapering cone, the apex of which is often bent and crooked, so that but little vestige of the three roots can be traced, the pulp cavity even being quite single.

Lower molars.—The first lower molar is the most constant in form, and is somewhat the largest; its grinding surface presents five cusps.

Four cusps are placed regularly at the four corners of a square, these being divided from one another by a crucial fissure ; the posterior arm of the crucial fissure bifurcates, and between its diverging arms is the fifth cusp, which is thus in the middle line and posterior.

The transverse fissure passes over the limits of the grind-

ing surface, and on the outside or labial surface of the tooth ends in a pit, which is a common site for caries; although it occasionally passes over the lingual surface, it is here less pronounced. They are implanted by two fangs, placed

Fig. 9 [1].

anteriorly and posteriorly; the roots are much flattened from before backwards, and they are very usually curved slightly backwards. In the median line of each root there is usually a groove, by the deepening of which four fangs may be produced; or this may happen with the one root only, so that a three-rooted tooth is the result.

Fig. 10 [2].

The second molar does not greatly differ from the first save that the roots are more often confluent, and the fifth cusp less marked, even if it exists at all.

[1] Masticating surface of a first lower molar, right side, the five cusps of which are indicated by figures.

[2] Second lower molar of right side, the four cusps being indicated by figures.

Third lower molar.—This tooth is seldom so small as the corresponding upper tooth, and its crown is often large even when its roots are very stunted. It has five cusps as a rule, and bears a more or less close resemblance to the molars which precede it. It is either two-rooted, or if the roots be confluent, a groove usually marks a tendency to division into two fangs.

It is stated by Prof. Owen ("Odontography," page 454), that although the wisdom tooth is the smallest of the three molars, the difference is less marked in the Melanian than in the Caucasian races, adding also that the triple implantation of the upper and the double implantation of the lower is constant in the former races. More extended observations have overthrown this statement as a positive dictum to be accepted without exceptions, but it may nevertheless be taken as expressing a general truth.

Fig. 11 (1).

The milk teeth differ from the permanent teeth by being smaller, and having the enamel terminating at the neck with a thick edge, so that the neck is more distinctly constricted. The incisors and canines are somewhat similar to their successors, the canines, however, being relatively shorter and broader than their successors. The first upper molars have three cusps, two external and one internal: the second more nearly resemble the permanent molars.

(1) Third lower molar of the left side.

The seeond lower deeiduous molar has four eusps and resembles a second lower permanent molar. The roots of the deeiduous teeth diverge from the neek at greater angles than those of permanent teeth, in eonsequenee of their more or less eompletely enclosing between them the erypts in whieh the latter are developing.

CHAPTER II.

THE MAXILLARY BONES.

The teeth are implanted in bone specially developed for the purpose; they lay at the period of their eruption in a wide excavation in the bone in which they were free to move under the influence of very slight forces, and the bone in which they are held was moulded around their roots subsequently to their being formed and moved into position.

The manner of attachment of the human teeth is that termed "gomphosis," *i.e.*, an attachment comparable to the fitting of a peg into a hole; the bony sockets, however, allow of a considerable degree of motion, as may be seen by examining the teeth in a dried skull, the fitting being in the fresh state completed by the interposition of the dense periosteum of the socket. This latter, by its elasticity, allows of a small degree of motion in the tooth, and so doubtless diminishes the shock which would be occasioned by mastication were the teeth perfectly immovable and without a yielding lining within their bony sockets. When this becomes inflamed and swollen by exudation the tooth is pushed to a certain extent out of the socket, and so being to a less extent limited in its range by the bony socket, acquires an increased mobility.

The teeth are in all mammalia confined to the bones which carry them in man, namely, the intermaxillary and maxillary bones and the lower maxillary bone or mandible.

While full description of these bones [1] will be found in any general anatomical work, there are a few points in their anatomy which directly concern the dental student, so that a brief enumeration of some of their relations can hardly be dispensed with.

Superior maxillary bone.—To facilitate description of its parts, anatomists divide it into a "body" and "processes," of which latter there are four, the nasal, malar, alveolar, and palatine. As the body of the bone is hollowed out by an air cavity, the antrum, its shape is similar to that of that cavity, namely, roughly pyramidal, the base of the pyramid being inwards towards the nasal chamber.

The nasal process springs directly upwards from the body in a vertical line with the canine tooth: it is a strong plate of bone, roughly triangular when viewed from the side.

The malar process forms the apical portion of the pyramid already alluded to; it starts out nearly horizontally from the body just behind and below the nasal process, and is characterized by its great strength and stoutness. Nevertheless it has been known to be fractured by a blow, and separated from the body of the bone. The antrum may be prolonged into it.

The palatine process forms a horizontal table projecting inwards from the body; as the floor of the nose is nearly flat, and the palate is arched from before backwards, the front of the palatine process is necessarily much thicker than the back, where it is quite a thin plate.

The alveolar process is a strong wide ridge of bone, curved so as to form with that of the other maxillary bone the elliptical figure characteristic of the dental arch in the higher races. It may be described as consisting of two plates, an outer and an inner, which are connected by numerous trans-

[1] Much that is of great interest, and that is not to be found in text books, is embodied in a series of papers on "The Facial Region," by Dr. Harrison Allen (American Dental Cosmos, 1873-74).

verse septa, the sockets of the teeth being formed by the interspaces between these septa. The internal alveolar plate is the stronger, the external the thinner and weaker, a fact of which we take advantage when we extract a tooth by bending it slightly outwards. On the outer surface of the alveolar process are eminences corresponding to the roots of the teeth, and depressions in their interspaces,

Fig. 12 (1).

apt to be especially marked over the canine teeth; while between the teeth the alveolar processes attain to a lower level, so that the margins of the bone are festooned. Looking down into an empty socket, the bone is seen to be everywhere very porous, and to be perforated by foramina of considerable size, while at the bottom there is the larger foramen admitting the vessels and nerves of the tooth.

The alveolus of each individual tooth consists of a shell of comparatively dense bone of small thickness, which is imbedded in a mass of loose spongy bone; this dense shell comes into relation with the dense cortical bone of the

(1) Superior Maxillary Bone of right side. 1. Body. 2. Tuberosity. 7. Malar process. 8. Nasal process. 12. Alveolar process.

jaw mainly at its free margin, near to the neck of the tooth. Over very prominent roots a portion of alveolus is at times wanting, so that in a macerated skull the root is exposed to view.

The upper maxilla serves to give form and support to the soft parts of the face, and also to carry the upper teeth. These have to be rigidly fixed, while the teeth of the lower jaw are brought forcibly against them with more or less of shock. And whilst these blows have to be received, and resisted, and ultimately borne by the cranium, it is obviously desirable that they should be distributed over a sufficiently wide area, so as not to be felt unpleasantly.

The ascending nasal process is very stout, and serves to connect the maxilla strongly with the frontal bone, which also in the region in question is powerfully developed; the thick malar process gives rigidity and resistance to lateral movements of the jaws, and carries off the strains to the lateral walls of the cranium; and the jaw is buttressed at the back by the pterygoid processes.

Taking next the various surfaces of the bone, there are four, or, if we include the palatine aspect, five: the external, forming a large part of the face, the superior or orbital, the internal or nasal, and the posterior or zygomatic. Upon the external or facial surface we have to note the eminence caused by the socket of the canine tooth ("canine eminence"), and immediately behind this a depression, the canine fossa, through which the antrum is sometimes punctured. The alveolar border, from the situation of the third molar to that of the second bicuspid, gives attachment to the buccinator muscle; while immediately beneath the margin of the orbit is the infra-orbital foramen, whence issues the infra-orbital nerve; hence this is one of the situations to which neuralgic pain really dependent on the teeth may be referred.

The orbital and nasal surfaces concern us only through their relation to the antrum, to be presently described; in the zygomatic surface, which is convex and forms part of the zygomatic fossa, are several orifices transmitting the posterior dental nerves and vessels; a groove which, converted by the apposition of the palate bone into a canal, forms the posterior palatine canal; and at the bottom, a rounded eminence, the maxillary tuberosity, which lies behind the wisdom tooth, and has been occasionally broken off in extracting that tooth.

The body of the bone is excavated by an air-chamber, the antrum, which is coated in life by a continuation of the nasal mucous membrane, and this frequently becomes secondarily involved in dental disease, so that its anatomical relations are of great importance to the dentist.

Like the somewhat similar air cavities in the frontal bone the maxillary sinus does not attain to its full size, relatively to the rest of the bone, until after the age of puberty, although it makes its appearance earlier than the other nasal sinuses, its presence being demonstrable about the fifth month of fœtal life. Hence it follows that its walls are thicker in the young subject than in the adult; and, according to the observations of Mr. Cattlin [1], it is somewhat larger in the male than in the female.

It is very variable in size, so that out of one hundred adult specimens the above-mentioned writer found one which would only contain one drachm of fluid, while in contrast with that was another which held eight drachms; two and a half drachms being the average capacity. Although it is exceedingly variable in form as well as in size, it tends towards a roughly pyramidal shape, the apex of the pyramid being directed towards the malar bone, which it has been seen to encroach upon, and the base towards the nasal cavity; it is, however, useless to minutely describe

[1] "Transactions of the Odontological Society," vol. ii. 1857.

its form, inasmuch as the two antra in the same individual are sometimes quite dissimilar. The floor of the cavity is rendered uneven in most specimens by prominences corresponding to the roots of the molar teeth, which ordinarily are but thinly covered by its bony walls, while it is not by any means rare to find some of them actually bare.

The cavity is also more or less completely subdivided by bony partitions springing from its walls, as is well exemplified in the accompanying figure; these partitions are for the most part thin, but they occasionally attain to considerable thickness, and they are stated to occur most frequently at the anterior or posterior angles of the base of the pyramid.

On the base of the pyramid is the orifice by which it opens into the middle meatus of the nose; this orifice being partly closed in by the ethmoid, palate, and inferior turbinated bones, and also by soft parts, so that in a recent

Fig. 13 (1).

subject it will barely admit a goosequill; and it should be noted that this orifice opens into the antrum near the top, so that it does not afford a ready means of egress to fluids accumulated in the cavity.

Through this orifice the mucous membrane lining the

(1) Section of an antrum of the left side, divided into many pouches by bony septa, and extending into the malar bone. Drawn from a specimen in the collection of Dr. Maynard, in the possession of the Baltimore Dental College.

antrum is continuous with that of the nasal fossæ, and, like that, it is ciliated; but it differs from the latter in being thinner and less vascular.

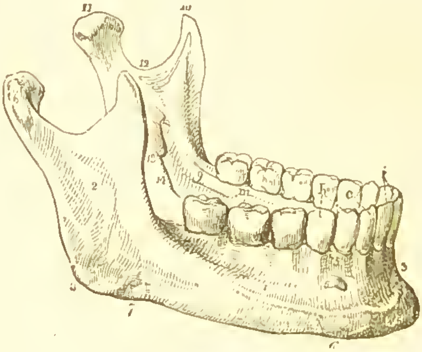
The teeth which usually come into the closest relation with the antrum are the first and second molars, but any of the teeth situated in the maxillary bone may encroach upon its walls, and I have seen an abscess, originating at the apex of the fang of a lateral incisor, pass backwards and perforate the antrum.

Its walls have four aspects, namely, towards the orbit, the nose, the zygomatic fossa, and the face, while its floor is formed by the alveolar border. With the exception only of the latter, its walls are very thin; and this exception has an important practical bearing in the diagnosis of tumors in this region, as accumulations of fluid or morbid growths really situated in the antrum bulge any or all of its walls in preference to the alveolar border, whereas tumors springing from the base of the sphenoid or elsewhere and encroaching upon the antrum, push down and distort the alveolar border as easily as any of the other walls of the cavity, inasmuch as the pressure caused by them is not transmitted equally in all directions, as is the case when the medium transmitting the power is a fluid.

The lower maxilla or mandible consists of a body and two rami, which ascend almost perpendicularly from its posterior extremity. The horizontal portion or body is curved somewhat in a parabolic form; it has a convex external and concave internal surface, and an upper (alveolar) and a lower border. On the convex facial surface we have to note the ridge marking the position of the symphysis, and below this the mental prominence. Externally to this, below the line of contact of the first and second bicuspids (or a little before or behind this point) is the mental foramen, which constitutes the termination of the inferior dental canal. Running obliquely upwards, and first visible

at a point a little distance from the mental prominence is the external oblique line, which becomes merged in the base

Fig. 14 (1).



of the coronoid process. Where it rises as high as the alveolar border, *i.e.*, opposite to the third and sometimes the second molar, the outer alveolar plate is strengthened by it, so that it becomes less yielding than the inner plate. The student should bear this fact in mind when extracting a lower wisdom tooth.

The buccinator is attached to the alveolar border opposite to the molar teeth ; the platysma myoides to the outer side of the lower border along a region somewhat further forward : the masseter over whole outer face and border of the ascending ramus and the temporal to the apex and side of the coronoid process. The other muscles attached to it are facial muscles of expression.

On the inner surface of the body are four tubercles, situated in pairs in the median line, about opposite to the ends of the roots of the incisors, but somewhat variable both

(1) Lower Maxillary Bone. 2. Ramus, where masseter is attached. 3. Symphysis. 5. Mental foramen. 6. External oblique line. 8. Angle of jaw. 9. Internal oblique line. 10. Coronoid process. 11. Condyle. 12. Sigmoid notch. 13. Inferior dental foramen.

in position and in size in different individuals. The upper pair of tubercles give attachment to the genio-hyo-glossus, the lower to the genio-hyoid muscles; they are interesting to the dental student not only as giving attachment to muscles concerned in deglutition, but as affording convenient fixed points for measurements of the relative growth of parts of the jaw. Beneath these genioid tubercles lie the slight depressions which give attachment to the anterior belly of the digastric muscle, while between the two points alluded to commences the internal oblique line, which runs obliquely upwards and backwards, becoming more pronounced as it extends backwards, and terminating at the inferior dental foramen. This internal oblique ridge marks the line of growth of the condyle (see Development of the Jaws), and gives attachment to the mylohyoid muscle, which forms the floor of the mouth, in all its length. Thus the bone above the ridge belongs strictly to the mouth, that below it has more relation with cervical structures. The depression for the sublingual gland is above this line, consequently this gland is visible from the mouth; that for the submaxillary gland is beneath it and further back.

The inner surface of the ascending ramus gives attachment to the following muscles: at the neck of the condyle to the external pterygoid; on the inner face of the coronoid process, as far down as the level of the top of the crown of the wisdom tooth, to the temporal; on the inner side of the angle, over a large surface, to the internal pterygoid.

The orifice of the inferior dental canal is rough and spinous, giving attachment to the internal lateral ligament of the jaw, while beneath and behind it is the groove for the mylohyoid vessels and nerves; the canal runs forward in the bone, a little distance beneath the ends of the roots of the teeth, and emerges at the mental foramen, turning outwards at an angle to reach it, and sending onwards small

canals to the incisors, not traceable far. It is nearer to the outer than to the inner surface of the jaw in the latter half of its course, and is apt to be very close to the ends of the roots of the wisdom teeth, and to those of the bicuspids. The alveolar processes of the lower jaw, at their posterior part, diverge more widely than those of the upper jaw, the relative antagonism between the upper and lower teeth being preserved in this region by the former having an inclination outwards, the latter inwards. The ascending rami join the body at an angle which is very obtuse in the fœtus, nearly a right angle in the adult, and once again obtuse in advanced old age; the explanation of this change will be given under the head of the Development of the Jaw.

The articulation of the human lower jaw is peculiar, and allows of a degree of play unusual in a joint. The ovoid condyles, when the jaw is at rest, are lodged in depressions, the *glenoid fossæ* of the temporal bone, formed partly by the squamous and partly by the vaginal portions of the bone. The posterior half of the cavity is rough, and lodges a portion of the parotid gland: the anterior is smooth, and is bounded in front by the *eminentia articularis*, which is the middle root of the zygoma, enters into the formation of the joint, and is coated over by cartilage. Between the condyle of the lower jaw, and the temporal bone lies a moveable *inter-articular fibro-cartilage*, which is an irregular bi-concave oval plate, the edges of which are united with the capsular ligament, so that the joint is divided into two cavities, furnished with separate synovial membranes (unless when, as sometimes is the case, the fibro-cartilage is perforated in its centre).

The joint is described as having four ligaments: the capsular, stylo-maxillary, internal and external lateral ligaments.

The capsular ligament is but feebly pronounced, and hardly deserves the name; the stylo-maxillary reaches from

the apex of the styloid process to the angle of the jaw ; the internal lateral from the spine of the sphenoid to the margins of the inferior dental foramen; the external lateral, which alone is a ligament strictly proper to the articulation, reaches from the outer side and tubercle of the zygoma to the outer surface of the neck of the condyle.

The form of the articulating surfaces and the comparative absence of retaining ligaments combine to allow of a variety of movement unusual in any other than a ball and socket joint. The articulation acts as a simple hinge when the jaw is simply depressed, and this is the only motion possible in many animals, as in typical carnivora. When, however, the mouth is opened to the fullest possible extent, the condyle leaves the glenoid cavity, slides forward, and rests on the articular eminence, the interarticular fibro-cartilage being carried forward with it. The passage of the condyle on to the articular eminence, although always taking place when the lower jaw is excessively depressed, takes place sometimes with but little depression of the lower jaw, which then passes horizontally forward; or it may take place on the one side only, giving to the jaw the lateral movement so useful in mastication. In the mastication of food the various movements are combined, or succeed one another with great rapidity ; the lateral movements are not very extensive, the outer cusps of the lower teeth of one side being brought to antagonise the outer cusps of the upper teeth, and then being made to slide forcibly down the sloping surfaces of the latter till they return to their normal antagonism ; when one set of muscles is tired the same process is gone through on the other side of the mouth.

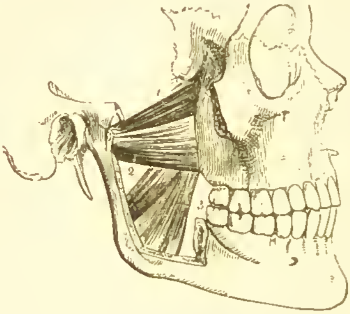
The closure of the jaw, and the rotatory and oblique motions, are accomplished by four pairs of very powerful muscles ; these are antagonised by muscles comparatively feeble and indirect in their application.

The closure of the jaws is effected by the masseters and

the temporals, attached to the outer sides of the jaw; and the external and internal pterygoids, attached to its inner sides.

The masseter, temporal, and internal pterygoid muscles close the jaws and press the teeth against one another, and

Fig. 15 [1].



this is their principal action. They are antagonised by the digastric, the mylohyoid, and the geniohyoid muscles, which, aided perhaps by the platysma, depress the lower jaw when the hyoid bone is fixed by its own depressor muscles.

The external pterygoid draws the jaw forward, and so in some measure tends to open it; as the two muscles do not always, or indeed generally, act together, they give a lateral movement to the jaw. The superficial portions of the masseter and the internal pterygoid are ordinarily supposed, as their direction is slightly backwards, to assist in drawing the jaw forwards, but Langer, a recent investigator of their action, attaches very little importance to this, and indeed considers that, when the jaw has been pulled forwards by the external pterygoid, the combined action of the internal pterygoid, the temporal, and the masseter, may bring it back again.

(1) Pterygoid muscles. 1. Upper, and 2. Lower heads of external pterygoid muscle. 3. Internal pterygoid muscle.

In ordinary mastication the various movements are combined in every possible manner.

When the mouth is widely open the condyles play upon the articular eminence in front of the glenoid cavity, and the external pterygoid, which assists in widely opening the mouth, draws not only the condyle, but also the interarticular fibro-cartilage forwards, so that the latter still intervenes between the condyle and the articular eminence. The interarticular cartilages do not, however, accompany the jaw in its extreme movement, but are believed only to pass forwards as far as that part of the eminence which is slightly hollowed out. As, however, in dislocation they accompany the condyles, this supposition may be incorrect.

The position of repose is neither complete closure nor opening of the jaws: in persons with enlarged tonsils the habitual position is one with the mouth somewhat more widely open, owing to the difficulty of breathing through the nose; a fact which often causes an irregularity in the disposition of the teeth.

The axis on which the jaw moves is, owing to the bend of the ramus, far behind the glenoid cavity; it lies very nearly in a plane formed by prolonging the plane of the masticating surface of the teeth.

The motions executed in mastication differ much according to the nature of the food; hence it happens that in different animals the muscles of mastication are very variously developed.

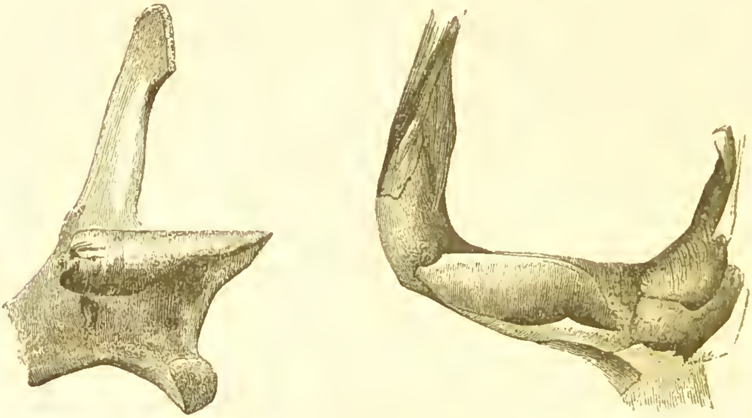
Thus, in the Herbivora, which move their jaws greatly from side to side, as anyone may observe for himself, the pterygoids, and especially the external pterygoid, attain to a very large relative size.

On the other hand, in the Rodents, which move their jaws backward and forwards in gnawing, tho masseter is enormously developed, and has a very marked general backward direction.

Although it is not strictly true, the masseter and temporal may be said in mammals to be developed in an inverse ratio to one another: when one is large the other is not.

The masseter is at a maximum in Carnivora, which have

FIG. 16 (1).



little lateral movement possible to their jaws; the temporal is also highly developed in many of the class.

In the great apes, the temporal becomes enormously developed only at the period of second dentition; this fact, conjoined with its size, which in herbivora seems to have some relation to the presence or absence of canines, would incline one to suppose that it was useful in that rapid closure of the mouth appropriate to biting when animals fight or seize prey.

The form of the glenoid cavity also bears an intimate relation to the dentition of the animal, and the nature and extent of the movement of its jaws.

Thus, in a child it is nearly flat, with no well marked surrounding elevations; its axis is transverse, and little rotary motion is made use of. In the adult it is deeply

(1) Condyle of the lower jaw, and glenoid fossa of a tiger.

sunk: the axis of the condyle is oblique, and rotary movements are largely made use of in triturating food.

In the Felidæ, it is strictly transverse; their teeth, adapted for slicing but not grinding, would gain nothing by lateral motion, which is rendered quite impossible by the manner in which the long transverse condyles are locked into the glenoid cavity by strong processes in front and behind. Curiously enough the interarticular cartilage is present, but as the condyle never moves forward, the cartilage is not attached to the external pterygoid muscle.

In Herbivora the condyle is roundish, the ascending ramus long, the pterygoid muscles large, and the glenoid cavity shallow; in the whale, which of course does not masticate at all, there is no interarticular cartilage, and no synovial membrane; the articulation is reduced to a mere ligamentous attachment.

The harder a substance is, the farther back between the molars it is placed; and as the food escapes from between the teeth it is constantly being replaced by the lips, cheeks, and tongue, the buccinator muscle being largely concerned in this work of preventing morsels of food from escaping from the teeth during its mastication.

Just as the muscles of mastication vary in their relative development in accordance with the food to be dealt with, so also do the salivary glands.

As a rule herbivorous creatures have large parotid glands; that is to say, those creatures which deal with the driest food and masticate it the most have this gland largely developed. For instance it is very large in Ruminants; in Herbivorous Marsupials it is larger, in the carnivorous section smaller, than the submaxillaries. When an especially viscid fluid is required, as, for example, that which lubricates the tongue of an ant-eater, this is furnished by exceedingly large submaxillary glands.

The face is to a very great extent modelled by the form

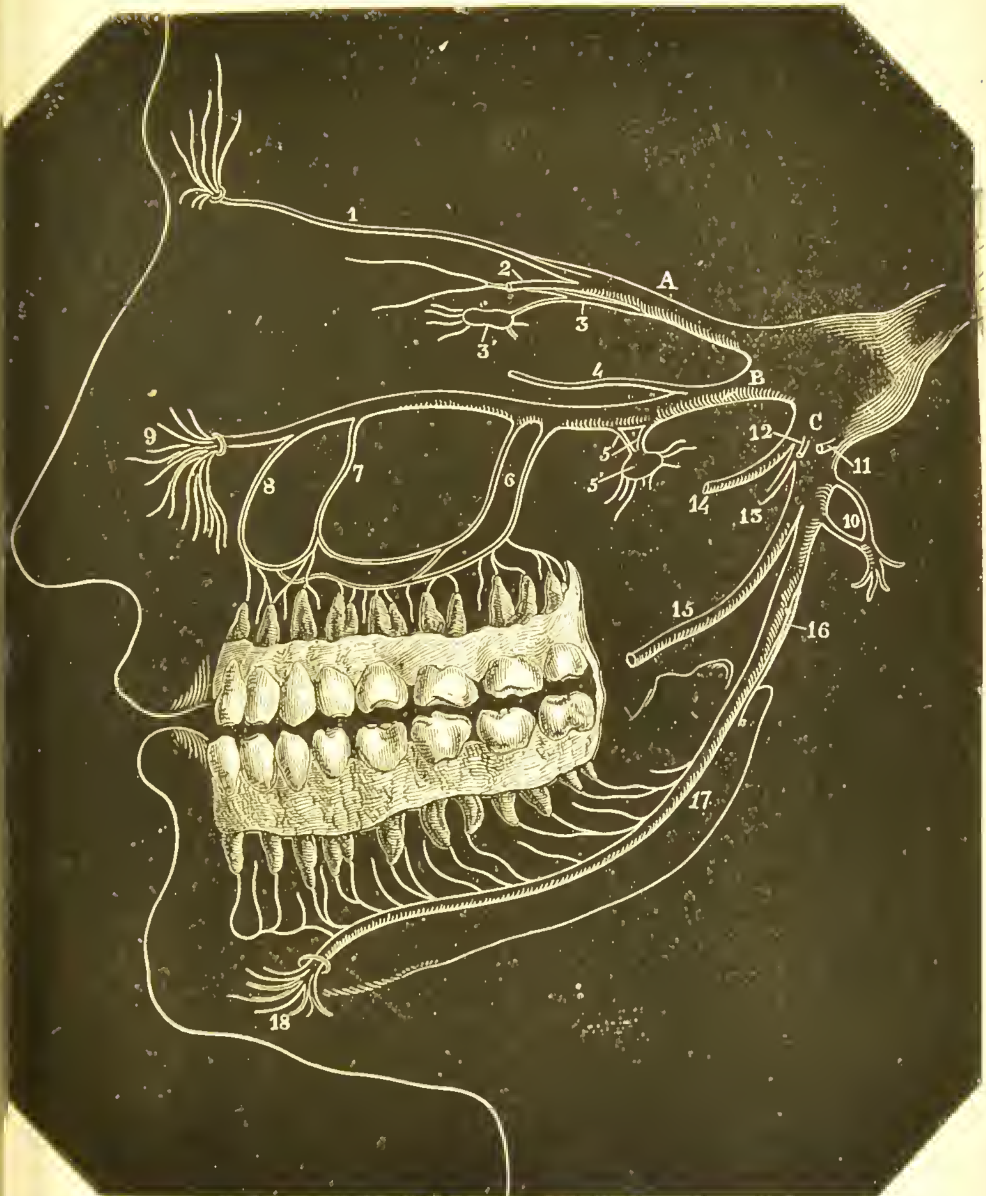
of the maxillary bones, and these again are found to be largely influenced by the dentition of the animal, so that it comes to be true to say that the face of an animal largely depends upon its dentition. Thus, to take a lion as an example, the snout is broad owing to the wide separation between the canines, which gives them a good purchase in grasping a living prey; its shortness enables them to be used at a greater mechanical advantage than would be the case were they further removed from their fulcrum at the joint, and the breadth of the face below the eyes is conferred by the widely spreading zygomatic arches, which are obliged to be wide to give passage to the very powerful temporal muscles, and attachment to the masseters.

Without going into further details, which the reader can readily supply for himself, it will be seen, therefore, that the contour of the face is largely determined by the dentition in this instance, and it is in marked contrast with the long thin snouts of the insectivora, whose forceps-like front teeth as a rule merely pick up unresisting prey, or with the long weak snouts of the horse and the herbivora generally. The face of the boar, again, is largely determined by the great muscles which move the jaw, and by the bony processes which give attachment to them.

If you extend the jaws forward a little, project the teeth, and widen the mouth in man, you get a coarse animal type of face; and, conversely, by a reduction of the maxillary region, perhaps even below the limits which will afford space for the regular disposition of the teeth, you get a refined oval type of face. The jaws of a negro are large relatively to the cranium, as are also those of exceptionally big men, such as we call giants, though this is not universally true: in rickets the reverse is the case.

The nerves of the teeth are derived from branches of the fifth nerve, the nerve of sensation of the whole side of the face and head: the lower teeth through the inferior maxil-

Fig. 17 (1).



(1) Diagram of the Distribution of the Branches of the Fifth Nerve.
(From Tomes' "Lectures on Dental Physiology and Surgery"—drawn by Mr. C. De Morgan.)

A. Ophthalmic division:—1. Frontal. 2. Nasal and long ciliary. 3. Branches to ciliary ganglion.

B. Superior maxillary division:—4. Orbital { temporal / malar } 5'. Sphenopalatine (Meckel's) ganglion. 6. Posterior dental, passing down. 7, 8. Anterior dental. 9. Infra-orbital.

C. Inferior maxillary division:—10. Auriculo-temporal. 11. Masseteric. 12. Deep temporal. 13. Pterygoid. 14. Buccal to buccinator, &c. 15. Gustatory. 16. Mylohyoid branch. 17. Inferior dental. 18. Mental.

[To face p. 40.

lary nerve, the upper through the anterior and posterior dental branches of the superior maxillary nerve. The nerves are given off from the nerve trunks in bundles corresponding in number to the roots of the teeth for which they are destined. For the details of the distribution of the fifth nerve the student must refer to works treating of anatomy, as it would be out of place to enter upon the subject at length in these pages, in which merely one or two matters of special interest to the dental student will be touched upon.

In the case of the inferior maxillary nerve the roots of the teeth come into very close proximity with the main trunk of the nerve; this is especially the case with the lower wisdom teeth. Within a few days of writing these lines I extracted a lower wisdom tooth (with forceps) for a gentleman, who, immediately after the extraction, inquired if he could have bitten his lip, as it felt swollen; on testing it I found slight but well marked numbness on that side of the lip and chin, which did not wholly subside before he left me. In this case a groove upon the under surface of the much curved roots appeared to indicate that the nerve trunk was in close contact with the tooth.

No reason is at present known why the tooth pulp should be so richly supplied with nerves, unless it confers greater tactile sensibility upon the whole tooth. Teeth with persistent pulps which go on growing throughout the life of the animal, have always large nerves: thus a very large trunk goes to the pulp of a rodent incisor. But although in this case the rich nervous supply doubtless has to do with nutrition, and presides over the great formative activity of the tissue, this does not fully account for the pulps of the teeth of limited growth being so amply supplied with nerves.

As has been mentioned in the description of the lower maxillary bone, the inferior dental nerve emerges from the bone by the mental foramen, near to the end of the roots of the bicuspid teeth. Pain due to distant causes is often

referred to the point of emergence of a nerve, as is so frequently exemplified in supraorbital neuralgia; in the same way pain due to diseased teeth far back in the lower jaw (especially to wisdom teeth), is frequently referred to the bicuspid region. Curiously enough, though there is no apparent close parallel in the disposition of the nerves, a similar reference of pain to the bicuspid region is occasionally observed in the upper jaw. And it may be added that there is very probably some closer parallel in the minute disposition of the nerve fibres going to the teeth in the upper and lower jaws than is recognisable by rough anatomical processes, for while, to all appearance, the nerve trunks are differently arranged, it is a matter of almost everyday observation to find pain due to one tooth referred with precision to its fellow in the other jaw.

The lower teeth derive their vascular supply from the branches given off to each tooth by the inferior dental artery, itself a branch of the internal maxillary; the upper teeth derive their arteries from the superior dental, a part of the alveolar branch of the internal maxillary, which supplies the molar and bicuspid teeth; and the front teeth from the descending branch of the infraorbital, the vessels thus having an arrangement somewhat analogous to that of the nerves.

The distribution of the veins corresponds closely to that of the arteries.

No lymphatics have been traced into the teeth, though lymph spaces are described by Dr. Black as existing in the alveolar dental periosteum.

TOMES, J. Lectures on Dental Physiology and Surgery. 1848.
HARRISON ALLEN. Anatomy of the Facial Region, Dental Cosmos. 1874.
CATTLIN. Anatomy of Antrum. Trans. Odontological Society. 1857.
BLACK. Periosteum and Peridental Membrane. Chicago, 1887.

CHAPTER III.

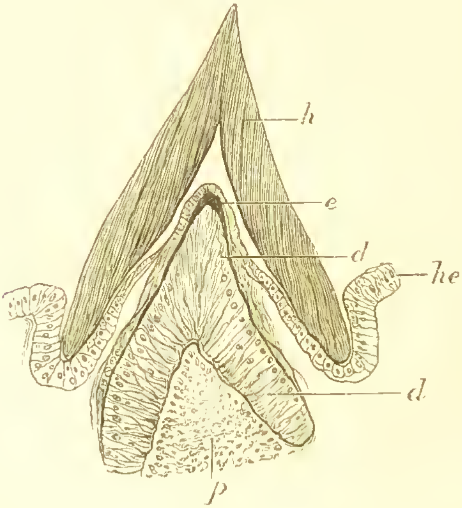
THE DENTAL TISSUES.

It is usual to speak of there being two kinds of teeth, namely, horny or albuminous, and calcified teeth; but the development of the former is not yet fully known, and it is hence impossible to determine the exact relation in which they really stand to other, or calcified, teeth.

The horny teeth of Ornithorhyncus have been shown to be purely epithelial, and to consist entirely of cells of the stratum corneum arranged in parallel columns which are penetrated by papillary processes of the oral epithelium. In other words they are an aggregation of long papillæ, in which the stratum corneum is abundant and hard, squeezed together to form a coherent mass. These horny teeth do the work of mastication during the greater part of the animal's life, but when the creature was half grown, it possessed true teeth with multi-cuspid grinding surfaces and short stunted roots. At that period the horny plates were not fully formed, but they were situated underneath the true teeth, and were incomplete only where the roots of the teeth passed through them. When the teeth were shed they became complete, but the peculiar sculpturing of their surfaces is due to their having once formed a bed for the short-rooted molars. But they are obviously not in any way homologous with true teeth. The horny teeth which surround the sucking mouth of the lamprey are found to consist of one or more superimposed horny cones,

standing upon a dermal papilla, and arising from a horn-producing groove around the base of the papilla (Beard, *Morphological Studies*, Jena, 1889). But the horny tooth of Myxine (the Hag) is yet more remarkable: in it the horny cone is superimposed, not upon a simple papilla, but upon a tooth germ which goes on to a considerable degree of calcification. Like the horny cones of the lamprey, its free edges rest in a horn-forming groove of oral epithelium. Inside this is a hard cone which appears to be a form of imperfect

FIG. 18 (1).



dentine (with vascular canals in it?): this Prof. Beard believes to be capped with enamel in one of his specimens, and in the interior of this is a pulp with odontoblasts. There is great difficulty in making out the structure, as these combined horny and calcified teeth almost defy ordinary methods of preparation.

The figure given above is somewhat diagrammatic, and is

(1) Tooth of Myxine. *d.* Dentine cap. *e.* Enamel (?). *h, e.* Horn forming epithelium. *p.* Pulp.

compounded from Dr. Beard's figures, and from a section which he was so kind as to lend me.

Between the horny cap and the dentine is an epithelial structure which is in the position of, and seems to play the part of, an enamel organ.

Calcified teeth are composed of one or more structures, which are in great measure peculiar to the teeth (although, what is to all intents and purposes dentine, is to be found in the skeletons and in the dermal appendages of some fish, and other exceptions might be found to the absolute accuracy of the statement), and hence are called "dental tissues." Notwithstanding the existence of certain transitional forms, it is not possible to doubt the propriety of a general division of dental tissues into three viz., Dentine, Enamel, and Cementum.

The first named of these constitutes the greater part of all teeth, and so far predominates in mass over the other constituents that, in very many cases, the tooth would retain its form and character after the removal of the enamel and cementum.

This central body of dentine, enclosing the pulp, is very often covered by a cap of enamel, which forms the surface of the tooth ; this may be very partial, as in the eel or the newt, in which animals only this enamel-capped tip of the tooth projects far above the surface of the mucous membrane : or it may cover a much larger proportion of the tooth, as in man. Perhaps the most usual condition is that the enamel invests the whole crown of the tooth, stopping short at about the level to which the gum reaches, as in the human and most other mammalian teeth of limited growth. In teeth of persistent growth the enamel extends down into the socket as far as the base of the tooth ; in such cases it may embrace the whole circumference of the dentine, as in the molar teeth of many rodents, or it may be confined to one side only, as in their incisor teeth, where by its greater

hardness it serves to constantly preserve a sharp edge as the tooth is worn away. The enamel is believed to be quite absent from many teeth; thus the subclass Edentata comprising sloths, armadillos, and ant-eaters have it not; the narwal, certain cetaceans, some reptiles, and many fish have none.

But although it might appear an exceedingly simple matter to determine whether a tooth is or is not coated with enamel, as a matter of fact in practice it is not always easy to be certain upon this point. When the enamel is tolerably thick there is no difficulty in making sections which show it satisfactorily, but when it is very thin it is apt to break off in grinding down the section. And even when it does not, it is in such cases usually quite transparent and structureless, and the outermost layer of the dentine being also clear and structureless, it is very hard to decide whether the appearance of a double boundary line is a mere optical effect due to the thickness of the section, or is indicative of a thin layer of a distinct tissue which might be either enamel or cementum.

My own investigations upon the development of the teeth of fish and reptiles have led me to suspect that rudimentary layers of enamel exist upon many teeth on which their presence has not been recognised, for I have found that the formative enamel organs occur universally, at least they exist upon all tooth germs which have been adequately examined. Upon the teeth of snakes, which were stated by Professor Owen to be composed only of dentine and cement, I have endeavoured to show that a thin layer of enamel exists, and that there is no cementum. The frog has an enamel organ as distinct as that of the snake, but I am hardly positive that there is enamel upon its teeth, although there is an appearance of a thin coat of distinct tissue. I have also demonstrated that the armadillo has an enamel organ, but have failed to discover any enamel or anything

like it upon its teeth, and Professor Sir Wm. Turner has made a similar observation upon the narwal.

At all events we may safely say that in these and many other creatures no functional development of enamel takes place: whether it does or does not exist in an extremely thin and rudimentary layer has become a question of much less significance, since I have shown the presence of an enamel organ to be probably universal at an early stage.

Hence I feel some hesitation in endorsing Professor Owen's generalisation that the dentine is the most and enamel the least constant of dental tissues; it is possible that it may be so, but recent researches into the development of teeth have very materially modified the conceptions formed as to the relations of the dental tissues to one another, and must lead us to examine carefully into such deductive statements before accepting them.

The remaining dental tissue is cementum, which clothes, in a layer of appreciable thickness, the roots of the teeth, and reaches up as far as the enamel, the edge of which it overlaps to a slight extent; when the cementum is present upon the crown, it occupies a position external to that of the enamel. Cementum occurs universally upon the teeth of mammalia, but it is not always confined to the root of the tooth; in many teeth of persistent growth it originally invested the whole crown, and after it has been worn from the exposed grinding surface, continues to invest the sides of the tooth. (See the description of the complex teeth of the elephant, cow, horse, &c.)

It is probably entirely absent from the teeth of snakes, and indeed of very many reptiles; in the reptilian class, at all events, it appears to me to be confined to those in which the teeth are lodged either in sockets or in a deep bony groove, as I am unacquainted with any tooth anchylosed to the jaw in which it exists, unless we are inclined to include under the

term cementum the tissue which I have designated "bone of attachment." (See "Implantation of Teeth.")

ENAMEL.

Upon the outer surface of the dentine the enamel forms a cap of a very much harder and denser material. In its most perfect forms it is very far the hardest of all tissues met with in the animal body, and at the same time the poorest in organic matter. In the enamel of a human adult tooth there is as little as $3\frac{1}{2}$ to 5 per cent. of organic matter, and, judging from its brittleness and transparency, there is probably even less in the enamel of some lower animals; the lime salts consist of a large quantity of calcium phosphate, some carbonate, and a trace of fluoride; in addition, there is a little magnesium phosphate.

Von Bibra gives two analyses of enamel:

	ADULT MAN.	ADULT WOMAN.
Calcium Phosphate and Fluoride .	89·82	81·63
Calcium Carbonate	4·37	8·88
Magnesium Phosphate . .	1·34	2·55
Other Salts	·88	·97
Cartilage	3·39	5·97
Fat	·20	a trace
Organic	3·59	5·97
Inorganic	96·41	94·03

Owing to the very small proportion of organic matter enamel when treated with a mineral acid wholly disappears, no organic framework being left behind. The structure of enamel, composed as it is of prisms of calcified material, is closely imitated in the invertebrate world by the shell of Pinna and many other molluscs, but these differ in several

respects, amongst others in having so large a proportion of organic basis as to retain a structure after decalcification. The cap of human enamel is of varying thickness, being thicker in the neighbourhood of cusps than elsewhere; in teeth of limited growth it terminates by a thin edge at the neck of the tooth, where it is overlapped to some slight extent by the cementum. When a thick coating of cementum exists over the whole crown, this lies outside the enamel, the proper place of which is therefore between the cementum and the dentine.

The external surface of human enamel is finely striated, the course of the striæ being transverse to the long axis of the crown; in addition to this very fine striation, there may be a few deeper and more pronounced grooves or pits, which are pathological, and are marks of checks in development more or less complete. The enamel of some animals is, to all appearance, structureless; such is the nature of the little caps which, like spear points, surmount the teeth of fishes of the eel tribe, cod tribe, or of the newt, and which from their extreme brittleness are often lost in preparing sections, so that their very existence has long been overlooked. But the absence of structure, if such it really be, is after all a mere question of degree; in the commonest form of enamel, such as that of the human teeth, there is a finely fibrous structure, very apparent in imperfect teeth, but far less so in well-formed ones, and the enamel of the eel is, in the manner of its development, fibrous; so that even though we cannot distinguish its constituent fibres when it is completed, this is merely an indication that calcification has progressed a little farther than in human teeth; if calcification only goes far enough, all structure, if not destroyed, will at all events be masked from sight.

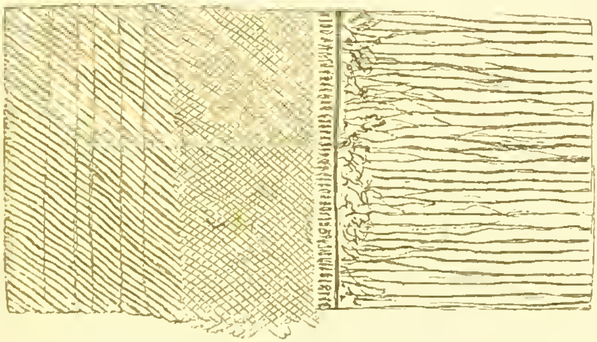
The structure of human enamel has been stated to be fibrous; that is to say, it has a cleavage in a definite direction, and is capable of being broken up into fibres or prisms

which seem in transverse section to approximate more or less closely to hexagonal forms brought about by their mutual apposition. The prisms run from the dentine towards the free surface; this is, however, subject to many minor modifications. The curved and decussating course of the human enamel prisms renders it difficult to trace them throughout their length, but the structure of the enamel of many lower animals (especially the rodents) is more easily intelligible. Enamel such as that of the Manatee, in which all the prisms pursue a perfectly straight course, is of comparatively rare occurrence; but among the rodents the courses pursued by the enamel prisms are simple, and produce very regular patterns, which are constant for particular families (J. Tomes). Thus, in the Sciuridæ, a section of the enamel, whether longitudinal or transverse, appears divided into an outer and inner portion, in which the prisms, although continuous from the dentine to the free surface, pursue different directions. As seen in longitudinal section, the enamel prisms start from the dentine at right angles to its surface, and after passing through about two-thirds of the thickness of the enamel in this direction, abruptly bend upwards, forming an angle of 45 degrees with their original course. In transverse section the enamel prisms are found to be arranged in horizontal layers, each layer being a single fibre in thickness; in alternate layers the prisms pass to the right and to the left, crossing those of the next layer at right angles, and thus making a pattern of squares in the inner two-thirds of the enamel. But in the outer third of the enamel, where the prisms bend abruptly upwards, those of superimposed layers no longer pass in opposite directions, but are all parallel; in fact no longer admit of distinction into laminæ.

Thus each enamel prism passes in a very definite direction, and, seen with those of other layers, forms a very characteristic pattern; but the enamel prisms are not in any part of their course curved.

In the beaver, from which the following figure is taken, the arrangement of the enamel prisms is dissimilar in the upper and lower teeth, the lamination taking place in different directions, so that a longitudinal section of the one might, so far as this is concerned, be mistaken for a transverse section of the other. As regards the decussation of

Fig. 19 ([1]).



the prisms of alternate layers, it is similar to that of the Sciuridæ, but it differs in the laminæ being slightly flexuous instead of pursuing perfectly straight lines.

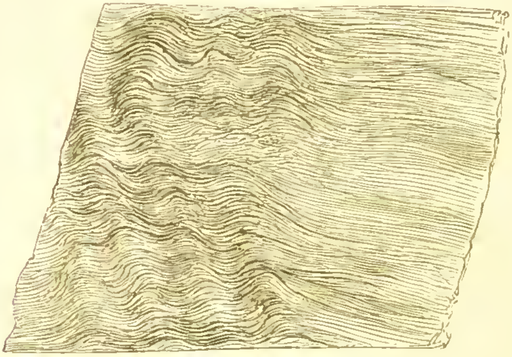
In the porcupine family very much more complex patterns are met with, the enamel prisms being individually flexuous, and their curves not being confined to one plane; the individual prisms pursue a serpentine course, and cannot be followed far in any one section. Near to the surface, however, they all become parallel, the enamel thus conforming with that of other rodents in being divided into two portions (at least so far as the course pursued by, and the pattern traced by, its fibres in its inner and outer parts can be said to so divide it). The Leporidæ, or hares, form an exception; their enamel has no such lamelliform

([1]) Section of dentine and enamel of a Beaver: in the inner half the prisms of contiguous layers cross each other at right angles, in the outer they are parallel.

arrangement, but is built up merely of slightly flexuous prisms.

By tracing the courses of enamel prisms from the simple pattern found in the Manatee through that of the squirrel, dormouse, and the porcupine, we see how a very definite arrangement, at first simple, becomes modified into something a little more complex, till at last it reaches a degree of complexity that looks like mere disorder. No one unfamiliar with the enamel of other rodents, looking at the

FIG. 20 (1).



enamel of the porcupine, would be able to unravel the very indefinite looking chaos of prisms before him; but had he studied forms in some degree transitional he could not doubt that the tortuous, curving course which he saw the prism to be pursuing was nevertheless perfectly definite and precise, and formed part of a regular pattern.

In perfectly healthy human enamel the fibrillar arrangement is not so very strongly marked; the prisms are solid, are apparently in absolute contact with one another, without visible intervening substance.

But Bödecker, basing his conclusions upon the examination

(1) Human enamel, from the masticating surface of a molar. The figure is merely intended to show the general direction of the fibres.

of thin sections stained with chloride of gold, holds that enamel is built up of columns of calcified substance, between which minute spaces exist. These are filled by a material which takes the stain deeply, and is probably analogous to the cement substance of epithelial formations. As seen in sections it gives off exceeding fine thorns, which apparently pierce the prisms at right angles to their length, so that it forms a close network very intimately mixed up with the calcified portion of the enamel.

It is not of uniform thickness, but is beaded, and Bödecker attributes it to a rôle of far greater importance than that of a mere cementing substance, for he regards it as being an active, protoplasmic network, which renders the enamel much more "alive" than it has hitherto been considered to be. He believes it to become continuous with the soft contents of the dentinal tubes through the medium of large masses of protoplasmic matter found at the margins of the enamel and dentine.

But although there are various reasons for suspecting that enamel is not completely out of the pale of nutrition from the moment that a tooth is cut, yet further observations are needed before the activity and importance of the cement substance demonstrated by Bödecker can be held to be fully established. Klein remarks that "the enamel cells, like all epithelial cells, being separated from one another by a homogeneous interstitial substance, it is clear that the remains of this substance must occur also between the enamel prisms; in the enamel of a developing tooth the interstitial substance is larger in amount than in the fully formed organ. It is improbable that nucleated protoplasmic masses are contained in the insterstitial substance of the enamel of a fully-formed tooth, as is maintained quite recently by Bödecker."

The study of the development of marsupial enamel, to be alluded to at a future page, by showing that the enamel is

penetrated by soft tissue differently placed, also tends to throw doubt upon Bödecker's interpretation. W. J. Barkas (*Monthly Review of Dental Surgery*, 1874) has perhaps had this cementing substance under observation; he also believes that the enamel prisms of human enamel are tubular, minute canals running along their axes.

On the whole the prisms are parallel, and run from the surface of the dentine continuously to that of the enamel. Their paths are not, however, either perfectly straight or perfectly parallel, for alternate layers appear to be inclined in opposite directions, while they are also wavy, forming several curves in their length. The curvature of the enamel prisms is most marked upon the masticating surface; while the layers, alternating in the direction of their inclination as just described, are in planes transverse to the long axis of the crown, and correspond to the fine striæ on the surface of the enamel, which appear to be caused by their outcrop. The curvatures take place in more than one plane; in other words, the course of the individual prism is more or less of a spiral.

Although most prisms run through the whole thickness of the enamel, yet inasmuch as the area of the outer is much larger than that of the inner surface of the enamel, and the individual prisms do not undergo any alteration in size as they pass outwards, many supplemental fibres are present in the outer portions of the enamel which do not penetrate far inwards.

The individual fibres are to all appearance structureless in perfectly formed human enamel, but a faint transverse striation, fainter, but otherwise not unlike that of voluntary muscle, is so general that it cannot be regarded as pathological, although it is most strongly developed in imperfect brownish enamel. The striation in question may be seen even in a single isolated fibre, and is not necessarily continuous over adjacent fibres, though it often is so; it is

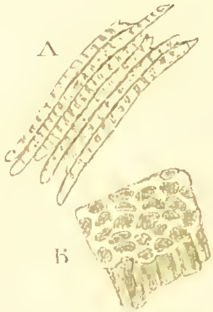
rendered more apparent by the slight action of diluted acids upon the fibre. Very various interpretations of this appearance have been given. It has been attributed to "an intermittent calcification" of the enamel fibre (Hertz), but is with more probability referred to varicosities in the individual fibres (Kölliker, Waldeyer) (1). It is very marked in the enamel of the common rat, which shares with that of other muridæ the peculiarity of having the individual fibres almost serrated, those of adjacent crossing layers being fitted to one another with great exactness. In human enamel the adjacent fibres, if united without any intermediate cementing medium, and pursuing courses slightly different, must of necessity be of slightly irregular form, or else interspaces would be left, which is not found to be the case. Thus the "decussation of the fibres" is a plausible explanation of this appearance of striation; indeed isolated fibres do present an appearance of slight varicosities, repeated at regular intervals. That the striation of enamel prisms is due to this cause is confirmed by Mr. Febiger, an American expert in the resolution of diatoms, to whom enamel sections were submitted for his opinion by Dr. Xavier Sudduth. The penetration, at regular intervals, of the prisms by the "thorns" of cement substance (see page 53), affords another possible explanation.

Although the perfect enamel fibre appears to be entirely homogeneous, it is not really so, for acids act with far greater rapidity upon the central or axial portion of the fibre than upon its periphery. The accompanying figure, taken from enamel softened by maceration in a $\frac{1}{4}$ per cent. solution of chromic acid, shows this well; the central portions of the fibre are dark, and are stained green by the reduced chromium sesquioxide, while the clear interspaces are

(1) The striation of voluntary muscle has been alleged to be due to this same cause (Dr. Haycraft, "Proceedings of Royal Society," Feb. 1881).

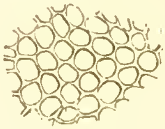
colourless. Again, if dilute hydrochloric acid be applied to a section of enamel, the axial part of the fibres are first attacked and are dissolved away, so that, if the section be transverse, a fenestrated mass remains. During the forma-

FIG. 21 (1).



tion of enamel the hardening salts are deposited first in the periphery of the enamel cells, so that the youngest layer of enamel is full of holes, each one of which corresponds to the centre of a fibre. Although calcification goes on to obliterate

FIG. 22 (2).



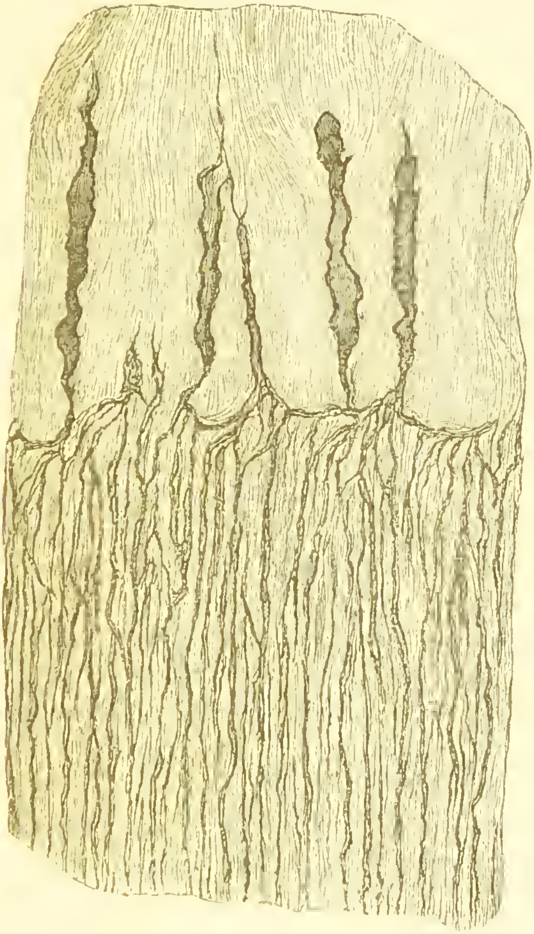
the visible difference between the centre and the periphery of the enamel fibre, yet the action of an acid reverses the order of its formation and once more makes it fenestrated, indicating that there is not absolute identity of substance in the inner part of the fibre. In imperfect enamel, indeed,

(1) From human enamel, softened in chromic acid, until it could be readily cut with a knife.

(2) Transverse section of enamel, the axial portion of the prisms having been removed by dilute hydrochloric acid.

a central narrow canal has sometimes been observed in the interior of an enamel fibre.

Fig. 23 [1].



In fractured enamel, the line of fracture is said to run through the centre of the fibres, and not, as might have been expected, through their interspaces; but this I have not verified.

[1] Cavities in human enamel, which communicate with the dentinal tubes.

There is also an appearance of striation upon a far larger scale, consisting of brownish lines, which are never, or very rarely, quite parallel with the outer surface of the enamel, but which nevertheless preserve some sort of parallelism with it and the surface of the dentine. These are known as the "brown striæ of Retzius," and, as they coincide with what was at one time the outer surface of the enamel cusp, are in some sense marks of its stratification in its original deposition.

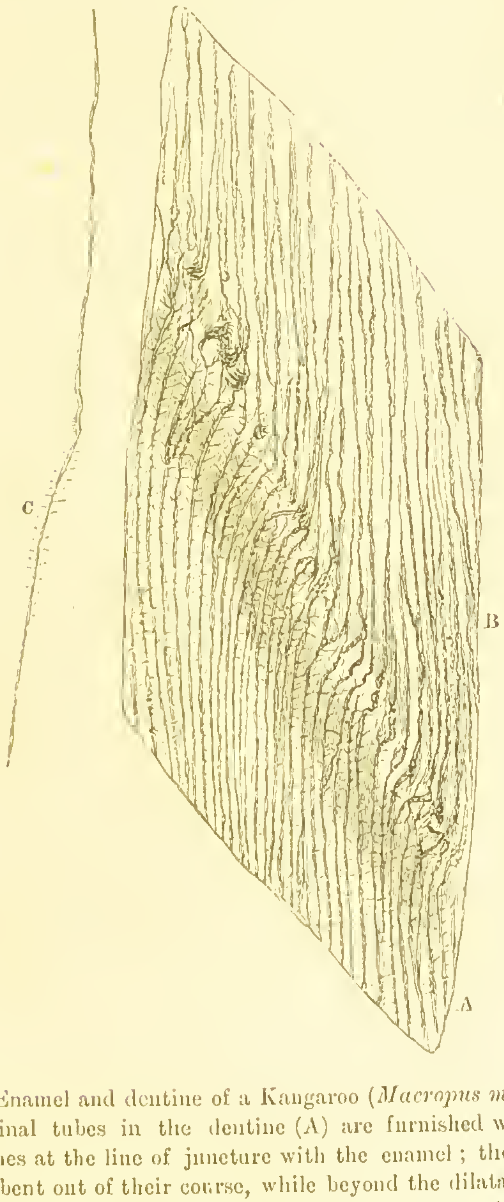
Pigment is seen in the enamel of many rodents; it is in the outer layers of the enamel, but has no sharply defined boundary, fading away gradually into the colourless tissue lying within it. Some authors have supposed that the pigment lay in a thin coating of cementum, or in a very distinct layer of enamel, but as has just been stated, such is not the case.

Cavities of irregular form sometimes exist in the enamel near to the surface of the dentine, and when such spaces exist the dentinal tubes sometimes communicate with them, but these are perhaps to be regarded as pathological: Bödecker regards them as filled up by protoplasm. Irregular fissures and cavities also occur upon the outer surface of the enamel, which also have no special significance save as predisposing causes of dental caries.

In man, however, dentinal tubes may occasionally be seen to enter the enamel, passing across the boundary between the two tissues, and pursuing their course without being lost in irregular cavities, though this appearance is seldom to be found. As was pointed out by my father, the passage of the dentinal tubes into and through a great part of the thickness of the enamel takes place in marsupials with such constancy as to be almost a class characteristic.

The only exception to the rule amongst recent marsupials occurs in the wombat, in which no dentinal tubes enter the enamel; those extinct marsupials which have been examined

Fig. 24 (¹).



(¹) Enamel and dentine of a Kangaroo (*Macropus major*).
The dentinal tubes in the dentine (A) are furnished with numerous short branches at the line of juncture with the enamel; they are dilated, and a little bent out of their course, while beyond the dilatation they pass on through about two-thirds of the thickness of the enamel in a straight course and without branches. Only a part of the whole thickness of the enamel is shown in the figure.

present, as might have been expected, a structure in this respect similar to that of their nearest allies amongst the recent genera.

The enamel of the wombat is peculiar also in another respect, being covered by a strong and remarkably uniform layer of cementum.

The penetration of the enamel by dentinal tubes is not, however, a peculiarity quite confined to the marsupials, for it is to be found in some rodents (*e.g.* the jerboa), and in some insectivora (*e.g.*, the Soricidæ).

Waldeyer and Hertz doubt the passage of the tubes of the dentine into the enamel; as Kölliker observes, it is difficult to see how they can doubt it, even after mere observation of a single specimen; moreover, it is also capable of experimental demonstration, for if an acid capable of removing the enamel be applied to one of these sections of marsupial teeth so as to dissolve away the enamel, the freed tubes are left hanging out from the edge of the dentine, thus putting the matter beyond all possibility of doubt. The enamel is also penetrated by dentinal tubes in some deep sea fishes.

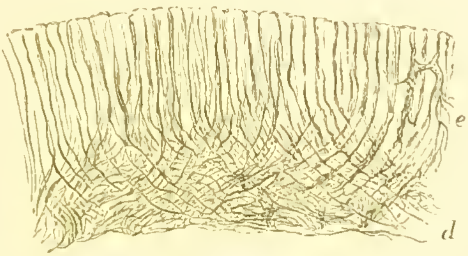
The most marked variation in the structure of enamel, which is on the whole a tissue differing but little in various animals, is met with in the class of fish.

In the Sargus, or sheep's-head fish, for example, the enamel is penetrated by a system of tubes which are not continued out of or derived from the dentine, but belong to the enamel itself.

The tubes, as seen in the figure, run at right angles to the external surface of the enamel, proceed inwards without branch or bend for some little distance, and then, at about the same point, bend abruptly at an angle, and give off numerous branches. The meshwork produced by the crossing of the tubes at all sorts of angles in the inner part of the enamel is so complicated as to render it impracticable to reproduce it in a drawing. That portion of enamel next

to the dentine is without canals. Von Boas (Zeits. f. wissen. Zoolog., Bd. xxxii.), describing the similarly constructed enamel of scaroid fishes, says that I was in error in supposing that the canals open upon the outer surface of the enamel. But I do not understand his reasons for dissenting

FIG. 25 (1).



from my opinion, which re-examination of many specimens has tended to confirm. I have not been able to satisfy myself whether the tubes occupy the interspaces of the enamel prisms, or their axes.

It would appear also as if these tubes were empty during life, as in sections they appear to be more or less blocked up with dirt. The existence of the prisms at all is not certain, and this led Kölliker to say that true enamel does not appear to exist in fishes (Mik. Anat. p. 114); the enamel of fish is, however, developed from an enamel organ homologous with, and exactly like, that of amphibia and reptiles, so that these anomalous tissues must be regarded as being unquestionably enamel.

(1) Enamel and dentine of the Sheep's-head fish (*Sargus ovis*). The enamel is penetrated by a system of channels which enter from its free exposed surface, pass in for a certain distance in straight lines, and then abruptly bending at an angle cross one another, and produce a complicated pattern in the inner third of the enamel.

DENTINE.

The dentine makes up the greater part of every tooth which thus, even after the removal of the other tissues, would preserve somewhat its characteristic form. Several varieties of dentine exist in which those peculiarities of structure which differentiate it from bone are less marked, so that a point is sometimes reached at which it is hard to say whether a particular structure should more rightly be regarded as dentine, or as bone. It will be most convenient to commence with the description of that variety of dentine which differs most markedly from bone; in other words, which has the most typical "dentinal" structure; and for that purpose the tissue met with in the teeth of man and the majority of mammalia, (though it is by no means confined to that class,) and known under the name "hard" or "unvascular" dentine, may be selected.

Dentine is a hard, highly elastic substance, in colour white with a slight tinge of yellow, and to some extent translucent, its transparency being often made more striking by contrast with the opacity which marks the first advent of dental caries. When broken a silky lustre is seen upon the fractured surfaces, which being in the main due to the presence of air in its tubes, is more apparent in dry than in fresh dentine; its fracture is sometimes described as finely fibrous.

The mass of the dentine consists of an organic matrix richly impregnated with calcareous salts; this matrix is everywhere permeated by parallel tubes, which run, with some deviations, in a direction at right angles to the surface of the tooth.

The Matrix.—The exact chemical composition of the matrix is not known; in man the proportion borne by the organic to the inorganic constituents varies in different individuals, and very probably in the same individual at

different ages, so that analyses can only give approximate results. In a fresh human tooth 62 per cent. of its weight was found to be inorganic salts, the tooth cartilage being 28 per cent., leaving a residue of 10 per cent. of water.

Von Bibra gives the following analysis of perfectly dried dentine :—

Organic matter (tooth cartilage)	27·61
Fat	0·40
Calcium phosphate, and fluoride	66·72
Calcium carbonate	3·36
Magnesium phosphate	1·18
Other salts	0·83

Von Bibra gives another analysis :—

Cartilage	20·42
Fat	·58
Salts	1·00
Magnesium phosphate	2·49
Calcium phosphate, and fluoride	67·54
Calcium carbonate	7·97

And Berzelius gives

Gelatine and water	28·00
Sodium salts	1·50
Magnesium phosphate	1·00
Calcium phosphate	62·00
Calcium fluoride	2·00
Calcium carbonate	5·50

The dentine of many mammals is very much more rich in magnesium phosphate than human dentine is; even the latter, it would seem, from the discrepancies existing between the various analyses, is variable in composition, but, on the whole, it may be said that, amongst inorganic

constituents of dentine, calcium phosphate largely preponderates; from $3\frac{1}{2}$ to 8 per cent. consists of calcium carbonate; a much smaller proportion consists of magnesium phosphate, while calcium fluoride exists in traces only.

The organic basis of the matrix is closely related to that of bone, with which however it is not identical; it is of firmer consistence, and does not really yield gelatine on boiling, but, according to Kölliker (who quotes Hoppe), the dentine of the pig yields a substance resembling glutin, the dentinal globules remaining undissolved. The animal basis of the dentine is called "dentine cartilage," and is readily obtainable by submitting a tooth for several days to the action of diluted acids. The form and most of the structural characteristics of a tooth so treated are maintained, the dental cartilage forming a tough, flexible, and elastic semi-transparent mass.

In the matrix of a perfect tooth no trace of cellular structure can be detected; it is uniform and perfectly transparent.

The Dentinal Tubes.—As has been already mentioned, the matrix is everywhere permeated by tubes, the precise direction of which varies in different parts of the tooth, so that the following description of their course must be taken as merely in a general way descriptive, and not as of universal or precise application. Each tube starts by an open circular mouth upon the surface of the pulp cavity; thence it runs outwards, in a direction generally perpendicular to the surface, towards the periphery of the dentine, which, however, it does not reach, as it becomes smaller, and breaks up into branches at a little distance beneath the surface of the dentine.

Near to the pulp they are so closely packed that there is little room between them for the matrix, while near to the outside of the tooth they are more widely separated: their diameter is also greater near to the pulp cavity.

The dentinal tubes do not pursue a perfectly straight course, but describe curves both on a larger and a smaller scale. The longer curves are less abrupt than the others, and are termed the "primary curvatures;" they are often compared to the letter *f*, to which they bear a certain amount of resemblance; the primary curves are more pronounced in the crown than in the root.

Fig. 26 (1).

The secondary curvatures are very much more numerous and are smaller; the actual course of the dentinal tube is, in many places at all events, an elongated spiral, as may be very well seen in thick sections transverse to the tubes; by alterations in the focus of the microscope the appearance of the tube making a spiral turn is made very striking. The effect of an elongated spiral viewed on its side will of course be only slight undulations, such as are the secondary curvatures of the tubes. The spiral course of the dentinal tubes is most strongly marked in the roots of teeth.

(1) Dentine and cementum of a Narwal, showing contour lines due to rows of interglobular spaces.

When a transverse section of dentine is viewed, bands or rings, concentric with the pulp cavity, are seen, and the same bands may be seen in longitudinal section. Such a striated or laminated appearance in the dentine may be due to two causes; and some little confusion has arisen in the nomenclature, owing to its double origin not having always been kept in view. Such striæ may be due to the presence of rows of interglobular spaces, or to the coincidence of the primary curvatures of neighbouring dentinal tubes: that is to say, each tube bends at the same distance from the surface, and the bend makes a difference in the optical properties of the dentine at that point.

Schreger described these latter: the lines of Schreger, therefore, are markings, ranged parallel with the exterior of the dentine, which are due to the curvatures of the dentinal tubes.

The "contour lines" of Owen, even in his own works, include markings of both classes: i. e., those due to the curvature of the dentinal tubes, and those due to laminæ of interglobular spaces, such as are met with in the teeth of Cetacea. Retzius had seen and described contour markings due to interglobular spaces, though his name is not usually associated with them, the "brown striæ of Retzius" being markings in the enamel.

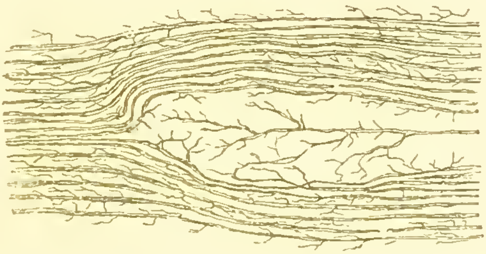
The tubes as they pass outwards often divide into two equally large branches; they also give off fine branches, which anastomose with those of neighbouring tubes. In the crown of a human tooth these fine branches are comparatively few, until the tube has reached nearly to the enamel, but in the root they are so numerous as to afford a ready means of distinguishing whence the section has been taken. The small branches above alluded to are given off at right angles to the course of the main tube, which, however, itself frequently divides and subdivides, its divisions pursuing a nearly parallel course.

The tubes are subject to slight varicosities, and their course is sometimes apparently interrupted by a small interglobular space, as is to be seen in an extreme degree in the dentine of Cetacea.

Owing to their breaking up into minute branches, some of the tubes become lost as they approach the surface of the dentine, and apparently end in fine pointed extremities.

Some terminate by anastomosing with terminal branches of others, forming loops near to the surface of the dentine; others terminate far beneath the surface in a similar way.

Fig. 27 (1).



Some tubes pass into the small interglobular spaces which constitute the "granular layer" described by my father, while others again pass out altogether beyond the boundary of the dentine and anastomose with the canaliculi of the lacunæ in the cementum.

The enamel also may be penetrated by the dentinal tubes, though this when occurring in the human subject must be regarded as exceptional and almost pathological in its nature (see Fig. 23). As has, however, been mentioned in speaking of the enamel, in most of the Marsupials and in certain other animals it is a perfectly normal and indeed characteristic occurrence, difficult though it be to see how such a relation of parts is brought about in the course of development of the two tissues.

(1) Termination of a dentinal tube in the midst of the dentine—human.

Dentinal Sheaths.—If dentine be exposed to the action of strong acid for some days, a sort of fibrous felt, or if the action of the acid has gone further, a transparent slime alone remains. Examined with the microscope this proves to be a collection of tubes ; it is, in fact, made up of the immediate walls of the dentinal tubes, the intervening matrix having been wholly destroyed.

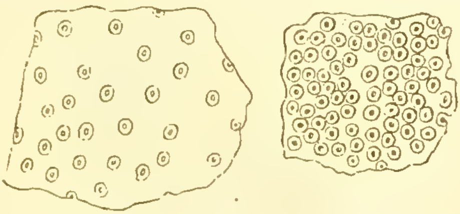
Two facts are thus demonstrated : the one that the tubes have definite walls, and are not simple channels in the matrix ; the other, that these walls are composed of something singularly indestructible. Indeed, the walls of the dentinal tubes are so indestructible that they may be demonstrated in fossil teeth, in teeth boiled in caustic alkalis, or in teeth which have been allowed to putrefy.

Although Kölliker was, I believe, the first to describe and figure these isolated tubes, they are generally known as the "dentinal sheaths of Neumann," the latter writer having more fully investigated and described them. The precise chemical nature of these sheaths will be more conveniently considered under the head of calcification : similarly indestructible tissues are, however, to be met with surrounding the Haversian canals and the lacunæ of bone. It is the opinion of Neumann, as it was also of Henle, that the dentinal sheaths are calcified ; but the proof of this is very difficult, as they cannot be demonstrated, or I should rather say, isolated, to any extent in dentine, unless it has been decalcified.. Their existence as distinct from the fibrils has been recently denied by Magitot and by Dr. Sudduth.

Transverse sections of dentine present fallacious appearances, owing to the thickness of the section giving to the tube a double contour which may be easily mistaken for a special wall. Immediately round the opening of the canal, or "lumen," as it is called, there is however generally a thin yellowish border, which may perhaps be the sheath of Neumann. In the earlier stages of caries, before the dentine is

much softened, the walls of the canals become strikingly apparent. But it must be remembered that the dentinal sheaths can only be demonstrated by processes which amount to a partial destruction of the dentine, and they are therefore in some degree at all events artificial, and it may be that they have no real existence until they are brought into existence by the action of these agents. In that case all that we are

Fig. 28 [1].



entitled to say, is, that the immediate surroundings of the soft fibril differ somewhat in chemical constitution from the parts of the matrix which are more remote, and so that under the action of destructive agents the matrix may be split up into the sheathing layers round the fibrils and the more soluble residuum of the matrix.

Dentine would thus be considered as a tissue made up of a calcified matrix, analogous to that of bone, permeated by the soft fibril just as bone is permeated by canaliculi with soft contents, but having this peculiarity, that the latest formed portions of matrix, namely, those immediately embracing the fibrils, differed sufficiently from the bulk of the matrix in chemical constitution to enable them to be isolated as sheathing tubes.

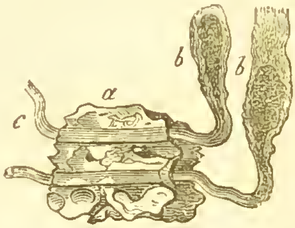
The canals which everywhere permeate the dentine are not empty, a fact which might be inferred from the difference in translucency and general aspect of dry and fresh

[1]) Transverse section of dentine. The appearance of a double contour is so much exaggerated as to make the figure diagrammatic.

dentine, whether seen in mass or in thin section; neither are they, as was at one time supposed, tenanted merely by fluid.

Dentinal Fibrils.—Each canal is occupied by a soft fibril, which is continuous with a cell upon the surface of the pulp; the existence of these soft fibrils was first demonstrated by my father, who thus, to use the words of

Fig. 29 [1].



Waldeyer, "opened the way to a correct interpretation of the nature of the dentine."

Henle, in his "Allgemeine Anatomie," (1841), a translation of a portion of which is to be found in the "Archives of Dentistry," (1865), figured and described projections from the edges of fragments of dentine in continuity with the dentinal tubes. These he distinctly describes as *calcified and rigid*, adding that by the use of acids they may be made flexible; he speaks of the tube as empty, save when blocked by granular calcareous matter, and alludes to fluids entering it by capillarity; and lastly, he says nothing whatever of the connections of the pulp with the tubes.

Müller, (as translated in Nasmyth on the "Structure of the Teeth," 1839), says, "in breaking fine sections of the teeth perpendicularly to the fibres, he has frequently seen the

(1) A fragment of dentine (*a*), through which run the softer fibrils (*c*), which are seen to be continuous with the odontoblast cells (*b*). (After Dr. Lionel Beale.)

latter projecting a little at the fractured edge. In such cases they are quite straight and not curved, and seem to be not at all flexible. Hence it follows that the tubes have an organised basis, a membrane, and that this is stiff and brittle, and probably saturated with calcareous salts, but weak and soft in a decalcified tooth."

The whole importance of my father's discovery lay in the fact that dentine is permeated by *soft, uncalcified structures;* and what is yet more significant, that these soft fibrils, permeating the hard dentine, proceed from the pulp. In no sense, therefore, did Henle anticipate this discovery.

In 1854 Lent figured processes from the dentinal cells (odontoblasts) which he rightly conceived to be concerned in the formation of dentine; but in the earlier editions of the "Histology" of his friend and teacher, Prof. Kölliker, although Lent's discoveries are described and adopted without reservation, no mention of the real structure of dentine occurs. But in the last edition, Prof. Kölliker says—"after Tomes had described a soft fibre in each tube, I fell into the mistake of supposing that these fibres and the tubes were one and the same."

The circumstances under which the dentinal fibrils can or cannot be discovered are as follows, and may be taken as indications of a distinction between the dentinal fibrils and the dentinal sheaths.

If a tooth section be submitted to the action of a caustic alkali and boiled in it, or be allowed to completely putrefy, so that the soft parts are entirely destroyed, the dentinal sheaths can still be demonstrated, but the fibres can in no way be brought into view (Kölliker). The dentinal sheaths may be demonstrated also in fossil teeth, as has been shown by Hoppe (Wurzburg Nat. Zeitschrift, Bd. VI. p. xi.) and others.

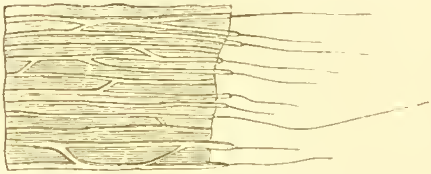
In fresh dentine every formative cell sends a process into the dentinal tubes (Tomes, Kölliker, Lent, Waldeyer, Neu-

mann), and it has been found possible to demonstrate both the sheaths and the fibres in the same sections (Neumann, Boll).

In transverse and even in longitudinal sections of decalcified dentine the fibrils may be recognised *in situ* (Kölliker).

The contrast between the dentinal sheaths and the fibrils is this :—the sheaths are very indestructible, and can be demonstrated in teeth which have undergone all sorts of change; the soft fibril is no longer demonstrable when the tooth has been placed in circumstances which would lead

FIG. 30 (1).



to its soft parts perishing. In dentine, then, we have (i.) a matrix permeated by canals; (ii.) special walls to these canals or "dentinal sheaths;" and (iii.) soft fibrils contained in these canals, or "dentinal fibres;" and it now remains to consider these in farther detail.

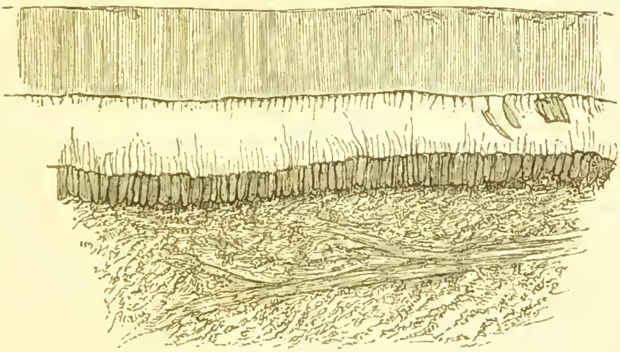
In fortunate sections of small fragments of dentine taken from the edges of the pulp cavity and including the surface of the pulp, the dentinal fibrils may be seen stretching from the cells of the superficial layer of the pulp (odontoblasts) into the dentinal tubes, as owing to these being extensile they may be stretched or drawn out from the tubes for some little distance without being broken across. In the same way they may be seen stretching across like harp-strings between two pieces of dentine, when this is torn by needles,

(1) Section of dentine from the edge of which hang out the dentinal sheaths, and beyond these again the fibrils (after Boll).

and they can be thus shown in fresh fragments just as well as in those of decalcified dentine. When stretched to a considerable extent their diameter becomes diminished and they finally break, a sort of bead sometimes appearing at the broken end (Tomes). This would seem to indicate that the substance of the fibril is of colloid consistency, and that its external portions are in some degree firmer than its axial portion.

The dentinal fibrils are well seen in the accompanying figure, in which some hang out from the edge of the dentine,

Fig. 31 (1).



whilst others have been pulled out from the dentine and are seen attached to the odontoblast cells.

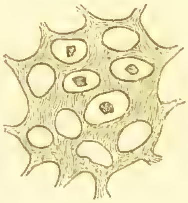
The dentinal fibril is capable of being stained with carmine, though with some difficulty ; in young dentine it is more easily stained, especially near the pulp cavity, and the accompanying drawing is taken from such a section of dentine from a half formed human incisor. The matrix is slightly stained with the carmine, indicating that it has not

(1) Surface of the pulp, with the odontoblast layer *in situ*. The dentine fibrils pulled out of the dentinal tube hang like a fringe from the odontoblast layer : dentine fibrils are also seen hanging out from the edge of the dentine, to which, to the right of the figure, a few odontoblasts remain attached.

yet become fully impregnated with salts, and in the centres of the clear areas dark spots deeply stained with carmine are to be seen, the latter being transverse sections of the dentinal fibrils *in situ*. I have observed precisely similar appearances in the thin young dentine of calves' and pigs' teeth; Kölliker also mentions that the dentinal fibril may be recognised *in situ* in transverse sections of fresh dentine.

Bödecker finds that the dentinal fibrils stain darkly with chloride of gold; when viewed in transverse sections under

FIG. 32 (1).



a magnifying power of 2,000 diameters they do not appear round but somewhat angular, and give off tiny lateral offshoots which seem to penetrate the dentine. In the matrix itself there is an appearance of a faint network when it has been stained with gold, and from this Bödecker infers that the dentine is penetrated everywhere by a network of living plasm, derived from, though far finer than, the dentinal fibrils.

Probably the angularity of the fibril, which, as figured by him, is much smaller than the canal, is due to its having shrunk under the action of chromic acid or some such reagent.

According to Neumann, in old age the fibrils atrophy or become calcified; some observers have failed to detect them

(1) Transverse section of dentine; in four of the dentinal tubes, the dentinal fibrils deeply stained with carmine, in the preparation from which this figure was drawn, are seen. The fibrils are somewhat shrunken, owing to the action of the glycerine in which the section is mounted.

near to the periphery of the dentine, far away from the pulp cavity. But here they would naturally be more minute, and it is more probable that the manipulations had failed to demonstrate them than that they were absent; for Bödecker has traced them to the very outside of the dentine.

Dr. Beale has seen prolongations of the nucleus of the cell towards the base of the fibril, though in the example which he figures it does not enter it.

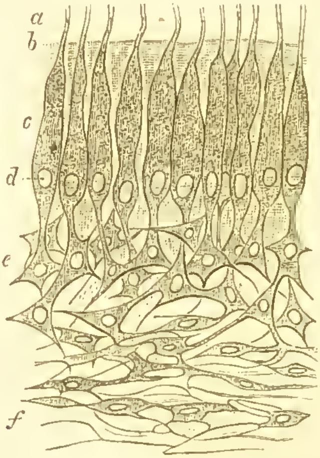
Dentinal fibrils have been demonstrated in the Reptilia and Amphibia by Santi Sirena and myself; and by myself in the few fish that I have examined with that purpose.

Of their real nature some doubts are entertained: they are certainly processes of the cells of the pulp, and their substance seems identical with that of the protoplasm of the cell. Nerves, in the ordinary sense of the word, they are not, and have never been supposed to be; but there are many examples of cellular structures which are connected with the termination of sensory nerve fibres, such as the goblet cells in the olfactory membrane of the frog, and it is quite possible that the odontoblast cells may stand in some such relations to the nerves of the pulp, the terminations of which have never been satisfactorily traced.

Mr. Coleman once suggested that it was possible that the odontoblasts might have some tactile function, and Mr. Hopewell Smith ("Dental Record," Aug., 1889,) points out their resemblance to multipolar ganglion cells of the spinal cord. According to Magitot the nerves of the pulp become continuous with a layer of reticulate cells which lie beneath the odontoblasts; and these freely communicate with the processes of the odontoblasts, so that there is a very direct chain of communication between the dentinal fibril and the nerves of the pulp. M. Magitot speaks very positively as to the accuracy of his views, which as yet, however, have not been confirmed by other investigators.

Yet another view of the nature of the dentinal fibril is advocated by Klein ("Atlas of Histology," p. 183), who holds that the odontoblasts are concerned only in the formation of the dentine matrix, and that the dentinal fibrils are long processes of the deeper cells, in the above

FIG. 33 ([1]).



figure, which run up between the odontoblasts and enter the dental canals.

In a recent paper (Comptes Rendus, 1880,) Magitot also impugns the accuracy of the views ordinarily accepted as to the structure of dentine, denying the existence of any special walls to the tubes, and further arguing that it is undesirable to think or speak of the channels in dried dentine as tubes at all. For, he argues, they are not tubes in the fresh state, seeing that the fibrils are adherent to the matrix and form a part of it, and that they were originally precisely the same tissue. He would prefer to speak of

([1]) After Magitot. *a.* Dentinal fibrils. *b.* Amorphous matrix. *c.* Odontoblasts. *d.* Nuclei of odontoblasts. *e.* Stellate cells. *f.* Nerve extremities which are continuous with the branched cells.

dentine as being a fibrillar tissue included in a hard and homogeneous matrix.

These views, however, do not differ substantially from those in the text, save that M. Magitot does not recognise the existence of that transitional tissue which others believe to be there, and call the sheaths of Neumann.

No true nerve fibril has ever been seen to enter the dentine; nothing but the dentinal fibril has ever been proved to pass from the pulp into the hard substance of the tooth; nevertheless, the observation of Boll is very suggestive. He found that by treating a perfectly fresh pulp with $\frac{1}{3}$ per cent. solution of chronic acid an immense number of fine fibres could be demonstrated, a great many of which projected from above the surface, as though they had been pulled out of the dentinal tubes; but although they pass up from a plexus of dark-bordered nerve fibres beneath the membrana eboris between the cells of that layer, their passage into the dentine remains a mere matter of inference.

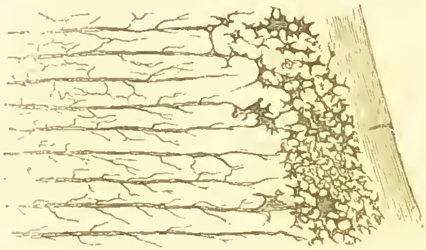
Boll's observations likewise are awaiting confirmation or disproof, and so far stand alone.

Be that as it may, there can be no question that the sensitiveness of the dentine is due to the presence of soft organized tissue in the tubes, and is not a mere transmission of vibrations to the pulp through a fluid or other inert conductor. The peripheral sensitiveness of a tooth can be allayed by local applications which it would be absurd to suppose were themselves conducted to the pulp; moreover, it is within the experience of every operator that after the removal of a very sensitive layer of caries, you often come down upon dentine, which, though nearer to the pulp, is far less sensitive, a condition quite inexplicable, except upon the supposition of a different local condition of the contents of the tubes. Irritation applied to the dentinal fibrils may be propagated to the pulp, and irri

tation of the pulp set up without any real exposure of the latter.

With reference to the probabilities of actual nerve fibres entering the dentinal tubes, it must be remembered that, in those tissues which are naturally so thin as to present great facilities for examination, nerves of a degree of fineness unknown elsewhere have been demonstrated ; in other words, the easier the tissue is to investigate, the finer the nerves which have been seen in it, while dentine is among

FIG. 34 (1).



the most difficult substances conceivable for the demonstration of fine nerve fibrils, if such exist in it.

Interglobular Spaces.—In the layer of dentine which underlies the cement an immense number of these spaces exist, giving to the tissue as seen under a low power an appearance of granularity. On this account my father gave to this the name of the "granular layer" of dentine ; on account of the far greater abundance of the spaces in that situation, it is far more marked beneath the cement than beneath the enamel, and many of the dentinal tubes end in these spaces.

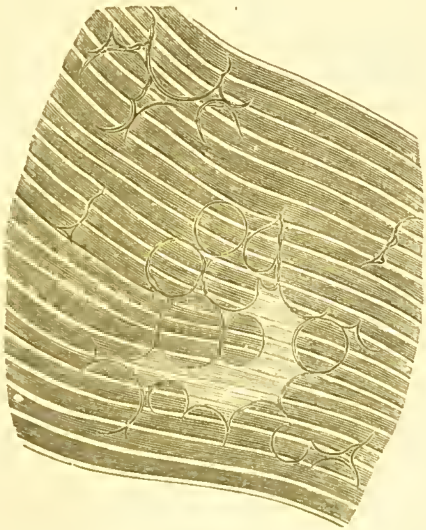
Although the name "interglobular spaces" is strictly applicable to the structures constituting the granular layer of dentine, it was not to these that it was first applied. When a dried section of dentine is examined, dark irregular

(1) Dentinal tubes terminating in the spaces of the granular layer.

spaces, clustered together and usually most abundant at a little distance below the surface, are often to be seen, particularly if the section has been made from a brownish, imperfectly developed tooth.

These spaces have a ragged outline, furnished with short pointed processes, and in favourably-prepared sections it may be seen that their outlines are formed by portions of the surfaces of closely opposed spheres, and globular contours may often be detected in the solid dentine near to

FIG. 35 (1).



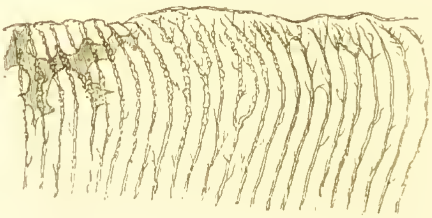
them, as is seen in the accompanying figure, taken from a section boiled in wax in order to render it very transparent.

Although these large spaces are very common, they are perhaps not to be regarded as perfectly normal, but are rather indications of an arrested development at that spot. The occurrence of globular forms during the early stages of calcification, will again be alluded to in connection with the development of teeth; but although the term "inter-

(1) Interglobular spaces in dentine.

globular" is thus strictly applicable, the use of the word "spaces" is not so correct. In dry dentine it is true that they are, as Czermak described them, spaces filled with air; but that they are so is only due to the fact that their contents are soft, and shrivel up in drying. In the fresh condition the interglobular "space" is perfectly full, its contents often having the structural arrangement of the rest of the matrix, or else consisting of soft plasm; in the former case, the dentinal tubes pass across and through

Fig. 36 (1).



it without any interruption or alteration in their course. This fact, as well as the soft nature of the contents as compared with the rest of the dentine, is well illustrated by a section in my possession which was taken from a carious tooth, near to the affected surface. In this the fungus, (leptothrix?), had effected an entrance into some of the tubes giving to them a varicose beaded appearance, and causing their enlargement. But when it reached the interglobular space, the less amount of resistance, or possibly the more favourable pabulum accessible, led to its more rapid development, so that the tubes within the confines of the space are many times more enlarged than those outside; nevertheless the continuity of the tubes across the space is well

(1) Section of carious dentine, in which some of the tubes are beaded by the ingress of the leptothrix, which has developed with greater freedom in one or two of the tubes where they cross the interglobular spaces.

demonstrated by the growth of leptothrix having followed them with exactitude.

It sometimes happens that indications of spherical forms and faintly discernible contours resembling those of the interglobular spaces may be seen in dried sections, in which no actual spaces occur. The appearances are perhaps produced by the formation of an interglobular space, the contents of which have subsequently become more or less perfectly calcified: the term "areolar dentine" sometimes applied to this is falling into disuse.

The exact nature of the contents of the interglobular spaces is not very certain: they may, with some difficulty, be tinted by carmine, and it is said that they may, like the dentinal sheaths, be isolated by the destruction of the rest of the matrix in acids; that this may be done I do not doubt, although I have never succeeded in so isolating them myself.

Bödecker finds that there is soft living plasm abundantly distributed in the smaller interglobular spaces which constitute the granular layer, and that this is in very free communication with the soft fibrils in the tubes on the one side, and with the soft contents of the lacunæ and canaliculi of the cementum on the other.

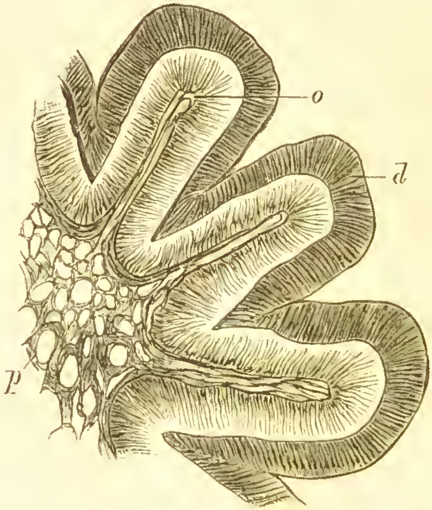
In the dentine so far described, which is that variety known as hard or unvascular dentine, some degree of nutrition is perhaps provided for by the penetration of the whole thickness of the tissue by protoplasmic fibres, the dentinal fibrils, but this nutrition may be effected in a different way, and there are other varieties of dentine known in which dentinal fibrils have never been shown to exist. For descriptive purposes I would classify dentines as

(i.) Hard or unvascular dentine.
(ii.) Plici-dentine.
(iii.) Vaso-dentine.
(iv.) Osteo-dentine.

Ordinary hard dentine has been sufficiently described; plici-dentine is a variety of it not very distinct in its essential nature, though at first sight widely dissimilar.

Plici-dentine.—In ordinary dentine the dentinal tubes radiate out from a pulp and pulp chamber of simple form; render complex that form by foldings of its walls, the dentinal tubes still running off at right angles to that portion

FIG. 37 (1).



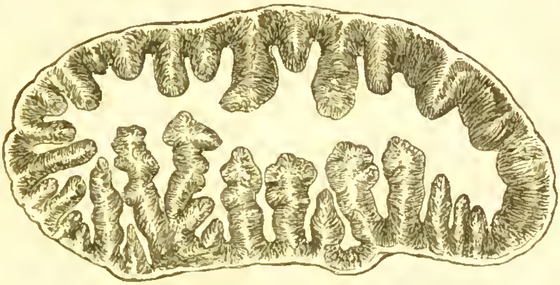
of pulp to which they immediately belong, and we have a "plici-dentine." It is merely an ordinary dentine with its pulp folded up and wrinkled into a greater or less degree of complexity.

In the teeth of the Varanus (monitor lizard) the process of calcification of the pulp takes place in such manner that in the upper half of the tooth a cap of ordinary unvascular dentine, in which the tubes radiate from a single central

(1) Section of Plici-dentine with the pulp *in situ* (Lepidosteus). *o*. Odontoblasts. *p*. Connective tissue framework of pulp. *d*. Dentine.

pulp cavity, is formed. But in the lower part of the tooth slight longitudinal furrows appear on the surface, which, on transverse section, are seen to correspond to dippings in of the dentine; and the dentine is, as it were, in folds. The pulp on section might be compared to a paddle-wheel, the floats of which correspond to the thin flat radiating pro-

FIG. 38 (1).



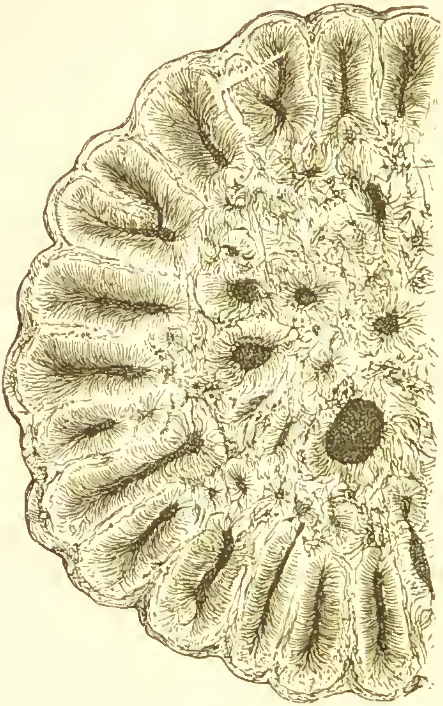
cesses of pulp; but as yet the central pulp chamber is unaltered. A little lower down, as represented in the accompanying figure, there is no longer a central simple pulp chamber; the inflections round the periphery have become relatively much deeper, and the centre of the tooth is occupied by a tissue irregular, but not otherwise unlike the dentine of Myliobates; that is to say, there are a number of columns of pulp, each of which forms the axis whence a system of dental tubes radiate.

The outrunning plates of dental pulp, which on section radiate out like the spokes of a wheel, do not always remain single; they may divide simply into two branches, as may be seen in the section across the base of the tooth of

(1) Transverse section across the crown of the tooth of Varanus, near to its base. The central pulp cavity is produced out into processes, and it might be said the dentine is arranged in plates with some little regularity round its periphery.

Lepidosteus (North American bony pike); or sometimes there are several branches.

FIG. 39 (1).



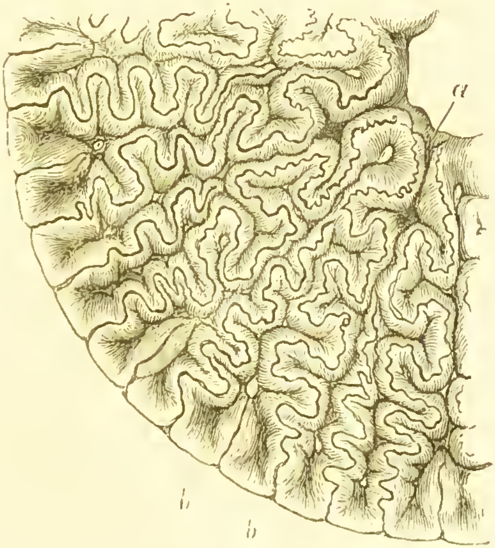
In Lepidosteus oxyurus there are simple inflections, and a central pulp cavity; in L. spatula the inflections are branched, and the central pulp cavity all filled up.

In the foregoing figure of the base of a tooth of Lepidosteus some few of the outrunning pulp chambers are

(1) Transverse section across the tooth of Lepidosteus spatula. At the exterior are regularly disposed radiating plates of dentine, each with its own pulp cavity, while the central area is composed of more or less cylindrical pulp chambers, each of which forms the starting point for its own system of dentinal tubes. The pulp chambers are made dark in the figure for the sake of greater distinctness.

seen to be bifurcated, while the central mass of the tooth is composed of dentine permeated by pulp canals which pursue a longitudinal course; a slight further modification brings us to the structure of the dentine of the Labyrinthodon, in which a maximum of complexity is attained, although a clue to its intimate structure is afforded by the teeth of Varanus or of Lepidosteus.

Fig. 40 (1).



The laminæ of pulp, with their several systems of dentinal tubes, instead of passing out in straight lines like the spokes of a wheel, pursue a tortuous course as they run from the central small pulp chamber towards the surface. Not only do they undulate, but they also give off lateral

(1) Transverse section of a tooth of Labyrinthodon. (After Owen.) The latter *a* is placed in the centre pulp chamber; the letter *b* marks the lines of separation between the system of dentinal tubes which belong to each lamina of pulp; these lines of demarcation were formerly supposed to be occupied by cementum.

processes; and at their terminations near to the surface of the tooth, the thin laminæ of pulp (so thin that the radiating pulp chambers are mere fissures) become dilated; so that on section circular canals are seen at these points, as is also the case at the points where subsidiary processes branch off

Fig. 41 (1).

The wavy course pursued by the radiating plates of dentine, and the disposition of the tubes round the dilated portions of pulp chamber, render the general aspect of the dentine structure very complicated; the several "systems" (2)

(1) From tooth of Labyrinthodon, showing the nature of the connection between the contiguous dentinal systems. (After a drawing of my father's.)

(2) The term "dentinal system" is applied to the portion of dentine in which all the tubes radiate from a single section of pulp chamber; thus the tooth of Labyrinthodon is made up of many dentinal systems; the same thing may be said of the tooth of Myliobates.

are united to one another by an inosculation of the terminal branches of the tubes in some few places, but more generally by a clear layer containing radiate spaces, something like the lacunæ of cementum. Hence Professor Owen has described the tooth as consisting of radiating plates of dentine, between which pass in equally convoluted plates of cementum. But, as was pointed out by my father (Phil. Trans. 1850), the mere presence of lacuna-like spaces is not sufficient to prove the presence of cementum, inasmuch as they occur on a small scale in the granular layer of dentine; moreover, when cementum and enamel are both present, the cementum is always outside the enamel, whereas at the upper part of the tooth of the Labyrinthodon the characteristic inflections take place within a common investment of enamel which does not dip in. Thus the whole of the tissue constituting the very complex pattern of the Labyrinthodon tooth is dentine, and the cementum does not, as was usually supposed, enter into its composition at all.

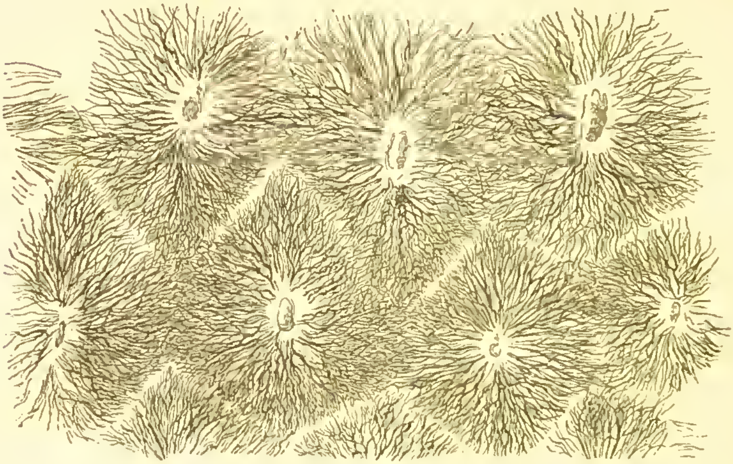
Another form in which plici-dentine may exist is exemplified in the teeth of Myliobates, a large Ray; or in the teeth of the rostrum of the saw-fish (Pristis).

In the Myliobates (Fig. 42) the flat pavement-like tooth is permeated by a series of equidistant parallel straight canals, running up at right angles to the surface; from the upper end and sides of these channels systems of dentinal tubes radiate, just as the tubes radiate from the single pulp chamber of a human tooth, save that they run for a comparatively short distance. In transverse sections the tubes are seen radiating from these channels, and at their terminations sometimes inosculating with the terminal branches of the tubes of another system. The channels contain prolongations of the vascular pulp, which are distinct in the upper part of the tooth, but intimately united together at its base, where the disposition of the channels ceases to be regular, and, as a consequence, the systems of dentinal tubes

pass from them in various directions without producing the symmetrical patterns which characterise the upper part of the crown.

When the tooth comes into use and its immediate surface

Fig. 42 (1).



gets worn off, the ends of the perpendicular pulp channels would be laid open, were it not that they become blocked by the deposition of a transparent homogeneous tissue within them, analogous to the similar tissue which closes Haversian canals of an antler about to be shed.

Such is an example of plici-dentine in a simple form, in which the tooth might be said to be built up of a series of small parallel denticles; and a similar structure is presented by the rostral teeth of the saw-fish, and by the teeth of the Orycteropus or Cape ant-eater.

Vaso-dentine.—In the dentine of human teeth it occasionally happens that a larger canal is found, having no clear relation to the course of the dentinal tubes, which it crosses at various angles; this larger canal contained the

(1) Transverse section of the dentine of Myliobates.

blood-vessel, the remains of which may be found even in a dried section. But in human dentine vascular canals do not often occur, and when they do, are to be regarded as decided abnormalities.

The accompanying figure, representing a canal of large

Fig. 43 ([1]).

size, was drawn from a specimen shown to me at the Cambridge (Massachusetts) Museum by Dr. Andrews.

In some mammalian teeth these vascular canals are disposed with regularity, running out in loops from the pulp cavity, and lying, for a considerable part of their course, at right angles to the dentinal tubes.

In the Manatee for example the dentinal tubes radiate out with perfect regularity from the central pulp chamber, and, so to speak, take no notice of the vascular canals,

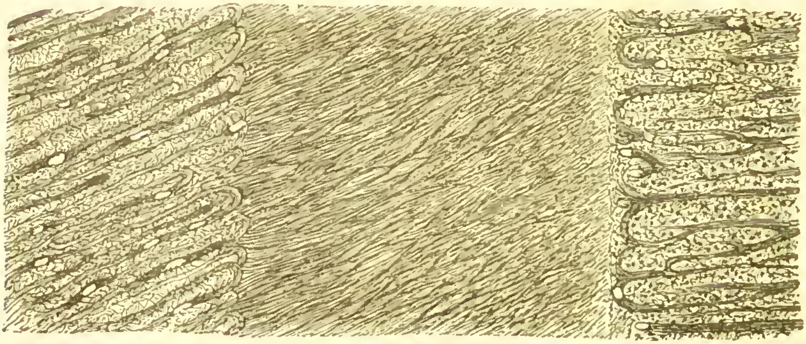
([1]) Vascular canal in dentine. From a human tooth.

which are to be met with (especially in the root) in large numbers.

Where they are numerous the vascular canals form loops, so as to constitute a sort of plexus beneath the cementum.

The Tapir, whose teeth in external configuration are not very dissimilar to those of the Manatee, also has vascular canals in the dentine; a curious difference in this respect

Fig. 44 (1).



was pointed out by my father (Proc. Zoolog. Soc. 1851) between the Indian and the American Tapir, the former having the canals in the dentine of the crown of the teeth, the latter having them not. The great extinct Megatherium possessed dentine very rich in these canals: to the left of the figure is seen the inner portion of the dentine, rich in them; in the middle a fine tubed dentine, forming the external layer of the dentine of the whole tooth, and to the right cementum, also rich in vascular tubes.

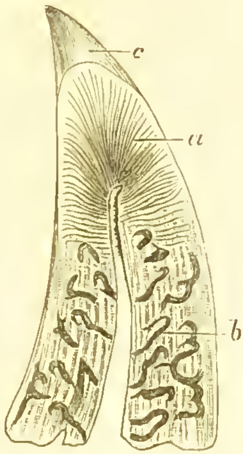
In those teeth in which the whole pulp is converted into solid material, and no pulp cavity remains, the last portions of the pulp are often converted into dentine which has not the same character as that of the rest of the tooth. Thus

(1) Dentine and cementum of Megatherium; the latter to the right of the figure.

in teeth of perpetual growth, such as the incisors of rodents, the axial portion of the tooth is that latest calcified, and consists of a dentine containing vascular canals, which are not present in the other part of the tooth. When a change thus occurs in the character of the tissue formed at a later time than the rest of the dentine, the name "secondary dentine" is applied to the resultant tissue.

But secondary dentine may partake of several different varieties of structure, so that the term must not be taken as

FIG. 45 (1).



denoting anything more than the circumstances under which it was formed.

It is in the class of Fish, in which vaso-dentine is rather common, that the most instructive examples of its nature are to be found.

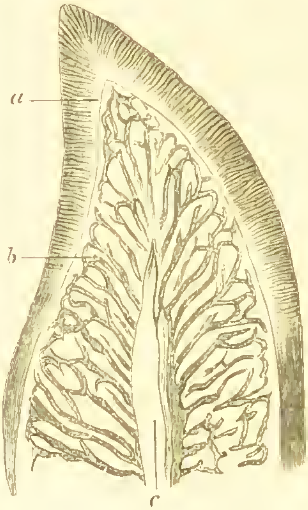
The conical teeth of the common Flounder, and indeed of most flat fish (Pleuronectidæ) have their pointed tips formed

(1) Tooth of a Flounder. *a*, Dentinal tubes near apex of tooth; *b*, Vascular canals; *c*, Spear points of enamel.

of ordinary hard dentine, surmounted by enamel tips. In this part of the tooth the dentinal tubes are numerous, and regular in their disposition, radiating out from the axial pulp chamber.

Lower down in the teeth the dentinal tubes become less numerous, and at the same time much larger looped canals make their appearance, and as these become more numerous

FIG. 46 (1).



and regular so do the dentinal tubes become less so. These larger tubes contain blood-vessels, and red blood circulates through them during the life of the tooth.

We may suppose that the nutrition of the dentine may be provided for either by protoplasm carried for a long distance from the pulp by the dentinal tubes, or by blood circulating through the larger vascular channels, but that both are not required, and so do not exist together.

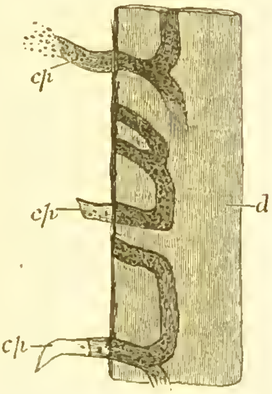
And whilst the teeth of the Manatee, the Tapir, and of

(1) Tooth of Ostracion. *a*, Enamel ; *b*, Capillary channels ; *c*, Axial m ber.

the Flounder teach that hard dentine and vaso-dentine are not very dissimilar in their nature, and that the one passes by imperceptible gradations into the other, the dentine at the base of the Flounder's tooth provides us with an example of typical vaso-dentine: that is to say, dentine in which the dentinal tubes are quite absent, having had their place taken by a complete system of vascular channels.

The teeth of the Ostracion (Fig. 46), or of the Hake (Figs. 47 and 89), afford good examples of this form of tissue.

FIG. 47 ([1]).



The matrix is solid, so far as penetration by fine tubes goes, but it contains a system of larger canals which carry only blood, and no pulp tissue, out to near the surface of the dentine, where they form a plexus.

I have not been able to satisfy myself of the existence of any definite structure in the matrix; sometimes it looks granular, and sometimes has a finely reticulated look, recalling the appearances described by Bödecker in human dentine. (See page 74.)

([1]) Section of Dentine from a freshly caught Hake (Merlucius). *d*, Dentine matrix; *cp*, Capillary blood-vessels hanging out from its edge, containing here and there abundant blood-corpuscles.

The arrangement of the vascular canals is regular and striking, reminding one of the appearance of the capillary network in an injected intestinal villus. In fact, an intestinal villus petrified, whilst the capillary network remained pervious and carried red blood circulating through it, would form no bad representation of a conical vaso-dentine tooth.

For these canals do actually contain capillaries, and blood actively circulates through them; a section cut from the fresh, brilliantly red tooth of a Hake often shows the coats of the capillary hanging out from the edge, and the canals full of blood corpuscles (Fig. 47).

In all vaso-dentine teeth with which I am acquainted the pulp chamber is of simple form, the pulp coated by a distinct layer of odontoblasts, and no pulp tissue other than the capillaries passing out into the dentine, so that each capillary fits and wholly fills its channel in the dentine.

Vaso-dentine is less dense and hard than ordinary dentine, and consequently generally gets protection by a harder tissue when exposed to hard work.

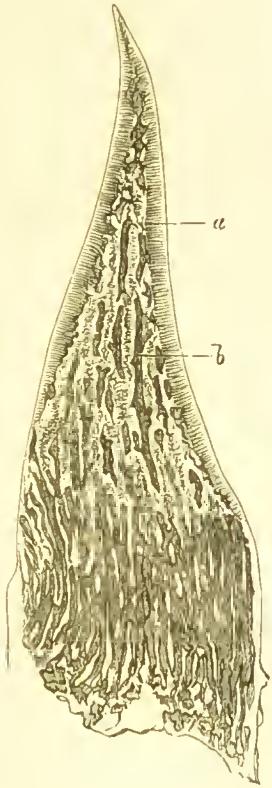
The teeth of the Hake, used simply for piercing and catching fish, are merely tipped with enamel (Fig. 89); those of Ostracion, put to severer work, are coated with enamel, while the teeth of the Wrasse (Labrus), which are composed of ordinary dentine are, though very hard worked, unprotected by enamel.

Osteo-dentine.—This is a tissue far more sharply marked off from hard dentine, plici-dentine and vaso-dentine, than these are from one another, and approaches closely to bone, from which it has few points of essential difference.

The distinction can hardly be fully emphasized until the development of dentine has been described, but it may be mentioned that it is not developed entirely upon the surface of the pulp, from an odontoblast layer, but within its whole substance. Consequently in a completed osteo-dentine tooth there is no single simple pulp, which can be withdrawn from

the tooth, but pulp and calcified tissue are quite inextricably mixed up.

Fig. 48 [1].



And though there are numerous large channels, often much larger than those of vaso-dentine, they are less regular, do not in their arrangement suggest the idea of capillary loops, and in a fresh tooth contain masses of pulp-structure as well as blood-vessels.

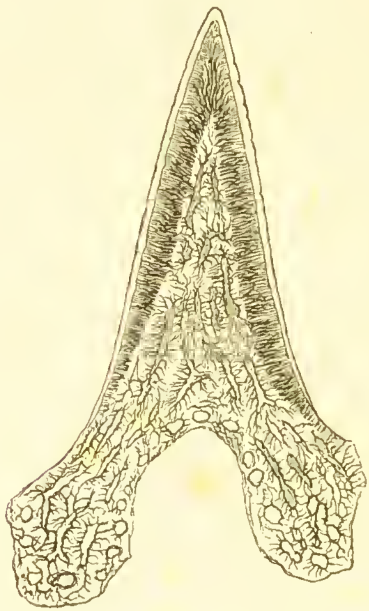
The Pike's tooth affords a good example of osteo-dentine. Its surface is formed of a layer of fine tubed tissue, almost

(1) Tooth of Common Pike. *a*, Outer layer of fine tubed dentine ; *b*, inner mass of osteo-dentine.

like ordinary dentine, but this soon gives place to a coarsely channeled tissue, containing elongated spaces filled with pulp, from which canaliculi, like those of a bone lacuna, branch off in all directions, but do not run far.

Very many sharks have teeth composed of osteo-dentine,

Fig. 40 ([1]).



with an outer dense layer: the tooth of Lamna here figured shows a central core of osteo-dentine, which constitutes the bulk of the tooth; external to this a somewhat thin layer of hard dentine, in which all the dentinal tubes run out at right angles to the surface, but are derived from the channels of the osteo-dentine and not from any single pulp chamber; while the outermost layer, which is clear and structureless,

([1]) Tooth of a species of Lamna, consisting of a central mass of vaso-dentine, passing towards its surface into a fine-tubed unvascular dentine. The clear structureless layer on the surface may probably be regarded as enamel.

may be merely the outer part of the hard dentine, or may be a thin layer of enamel. It is to be regretted that special names have been given to this layer; it is sometimes called vitro-dentine, sometimes ganoin or fish-enamel; but there is no reason why it should have a special name at all. The similarity of the channels of pulp in osteo-dentine to Haversian canals in bone is very close; in fact, when teeth consisting of osteo-dentine become, as in many fish they do, anchylosed to the subjacent bone, it becomes impossible to say at what point the dentine ends and the bone commences; and this difficulty is intensified by the fact that the bone of many fishes lacks lacunæ, and is almost exactly like dentine.

Osteo-dentine was defined by Professor Owen as dentine in which the matrix was arranged in concentric rings around the vascular canals, and in which lacunæ similar to those of bone were found.

But neither of these characters are to be found in many teeth, which, if the manner of their development is to be taken into account, are unquestionably made of osteo-dentine; and so they cannot be made use of for purposes of definition, although lacunæ and lamination of the matrix are far more often present in osteo-dentine than in the other varieties of dentinal structure.

The varieties of dentine may be grouped thus:—

(A.) Dentines developed upon the surface of a pulp, by calcification of a specialised layer of odontoblast cells.

(i.) Hard, unvascular dentine, thoroughly permeated with dentinal tubes, which radiate from a simple central pulp chamber. Example—Human dentine.

(ii.) Plici-dentine, permeated with dentinal tubes, which radiate from a pulp chamber

rendered complex in form by foldings in of its walls. Example—Lepidosteus, Labyrinthodon.

(iii.) Vaso-dentine, dentinal tubes few or absent, but capillary channels with blood circulating through them abundant. Example—Hake.

(B.) Dentines developed by calcification shooting through the interior of a pulp, not by calcification of a specialised surface layer of cells.

(iv.) Osteo-dentine; with no long dentinal tubes, but minute tubes analogous to bone canaliculi, and large irregular channels containing pulp-tissue (not blood-vessels only). Example—Pike.

It remains to be added that the same pulp may undergo a change in the manner of its calcification; that is to say, that after having gone on with surface calcification from an odontoblast layer for a certain length of time, this may give place to a more irregular internal calcification into an osteo-dentine.

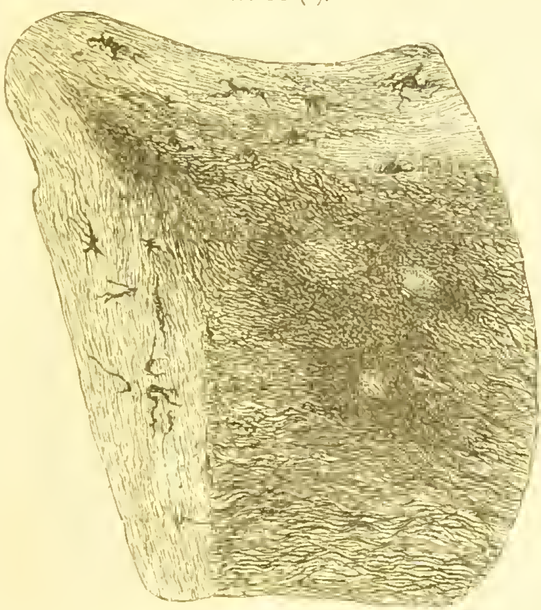
This is especially prone to happen after injury, and is often exemplified upon a large scale in Elephants' tusks; the pulp of which, normally engaged in calcifying the odontoblast layers into ivory, may after an injury calcify irregularly, and solidify into a coarse osteo-dentine.

It will then be easy to understand that so-called secondary dentine, produced in a pulp which ordinarily forms hard dentine, may partake of the character of vaso- or of osteo-dentine.

Thus the pulp of a sperm whale's tooth becomes obliterated by a development of secondary dentine, which sometimes forms irregular masses loose in the pulp chamber, and sometimes is adherent to and continuous with the dentine

previously formed. The structure of these masses is very confused. Tubes, of about the same diameter as dentinal tubes, abound; but they are often arranged in tufts or in bundles, and without any apparent reference to any com

Fig. 50 [1].



mon points of radiation. Irregular spaces, partaking of the character of interglobular spaces or of bone lacunæ, abound; and vascular canals are also common.

In the human tooth secondary dentine occurs in the teeth of aged persons, in which the pulp cavity is much contracted in size, and is also very frequently formed as a protection to the pulp when threatened by the approach of dental caries, or by the thinning of the walls of the pulp cavity through excessive wear. The following figure, representing one of the cornua of the pulp chamber from a molar tooth affected by caries, is a good example of secondary dentine

[1] Section of a mass of secondary dentine from the tooth of a sperm whale.

It occasionally happens that the pulp resumes its formative activity, and new dentine is developed which, with the exception of a slight break or bend in the continuity of the tubes, is almost exactly like normal dentine. More often,

FIG. 51 (1).

however, the boundary line between the old and the new is marked by an abundance of irregular spaces and globular contours, whilst further in the mass of new secondary dentine, the tubular structure again asserts itself more strongly: this is well seen in the specimen figured.

THE TOOTH PULP.

The pulp occupying the central chamber or pulp cavity, was the formative organ of the tooth, and consequently varies

(1) Secondary dentine filling up one of the cornua of the pulp cavity. From a human molar affected by caries.

in its anatomical characters according to its age. As well as being what remains of a formative organ, it is the source of vascular and nervous supply to the dentine.

The pulp may be described as being made up of a mucoid gelatinous matrix, containing cells in abundance, which are especially numerous near to its periphery. In it some fibrous connective tissue is discoverable, though this is not abundant until the period of degeneration has set in. Nerves and vessels also ramify abundantly in it.

The matrix substance remaining in large proportion, whilst the cell elements are not greatly developed, and the fibrous element being still less conspicuous, gives to the pulp the character common to many embryonal tissues.

In some specimens prepared by Mr. Mummery, in which the pulp *in situ* is impregnated with hardened balsam, and the whole cut and rubbed down subsequently, there is an appearance as though the matrix substance against the dentine had a sort of fenestrated structure, and as if bands of it ran into the dentine (cf. Sharpey's fibres in cementum).

I had myself observed some indication of a similar appearance in pulps which had been differently treated, yet it is by no means certain how far it is due to method of preparation, nor whether this may not be half formed dentine which takes on this appearance.

The cellular elements of the pulp are arranged, as seen in transverse sections, in a direction radiating outwards from the centre; this is most marked in the highly specialised layer of cells which form the surface of the pulp, and are termed *odontoblasts.*

The odontoblast layer, sometimes called the *membrana eboris*, because it usually adheres more strongly to the dentine than to the rest of the pulp, and is therefore often left behind upon the dentine when the pulp is torn away, consists of a single row of large elongated cells, of darkish

granular appearance, with a large and conspicuous nucleus near to the end farthest from the dentine.

The sharp contours which the odontoblasts possess in pulps which have been acted on by chromic acid, alcohol, or even water, are absent in the perfectly fresh and unaltered condition, and it is believed that they have no special investing membrane. They are furnished with three sets of processes. The *dentinal process* (which is equivalent to the dentinal fibre) enters the canal in the dentine, and the individual odontoblast may be furnished with several dentinal processes. By means of *lateral processes* the cells communicate with those on either side of them, and by means of their *pulp processes* with cells lying more deeply; these deeper cells again are to some extent intermediate in size between the odontoblasts and the internal cells of the pulp. The membrana eboris covers the surface of the pulp like an epithelium. The odontoblasts vary much in form at different periods; in the youngest pulps, prior to the formation of dentine, they are roundish, or rather pyriform; during the period of their greatest functional activity the end directed towards the dentine is squarish, though tapering to a slight extent into the dentinal process; while in old age they become comparatively inconspicuous, and assume a rounded or ovoid shape. The general matrix of the pulp, as has been before noted, is of firm, gelatinous consistency: it is a little more dense upon the surface, whence has perhaps arisen the erroneous idea that the pulp is bounded by a definite membrane.

The vessels of the pulp are very numerous; three or more arteries enter at the apical foramen, and breaking up into branches which are at first parallel with the long axis of the pulp, finally form a capillary plexus immediately beneath the cells of the membrana eboris.

No lymphatics are known to occur in the tooth pulp.

The nerves enter usually by one largish trunk and three

or four minute ones: after pursuing a parallel course, and giving off some branches which anastomose but little, in the expanded portion of the pulp they form a rich plexus beneath the membrana eboris, as has been described by Raschkow and many subsequent writers.

But here our exact knowledge ends, for the nature of the terminations of the nerve fibres in the pulp is not with certainty known: the primitive fibrils, which are extraordinarily abundant near to the surface of the pulp, often form meshes, but this does not appear to be their real termination.

Boll, as has been mentioned at a previous page, investigated this point, and found that if a pulp be treated for an hour with very dilute chromic acid solution, an immense number of fine non-medullated nerve fibres, which he succeeded in tracing into continuity with the larger medullated fibres, may be discerned near to the surface of the pulp. The ultimate destination of these nerve fibres is uncertain; but he has seen them passing through the membrana eboris, and taking a direction parallel to that of the dentinal fibrils in such numbers that he infers that they have been pulled out from the canals of the dentine. Still, whatever may be the probabilities of the case, he has not seen a nerve fibre definitely to pass into a dentinal canal, nor has any other observer been more fortunate.

Boll's observations have not however been fully confirmed by any subsequent worker in the field, nor had they been definitely controverted until Magitot recently stated that he had fully satisfied himself that the nerves become continuous with the branched somewhat stellate cells which form a layer beneath the odontoblasts, and through the medium of these cells with the odontoblasts themselves. (See Fig. 33.)

If this view of their relation to the nerves be correct the sensitiveness of the dentine would be fully accounted for without the necessity for the supposition that actual nerve

fibres enter it, for the dentinal fibrils would be in a measure themselves prolongations of the nerves.

It has already been mentioned that the pulp undergoes alterations in advanced age, its diminution in size by its progressive calcification and the addition thus made to the walls of the pulp cavity being the most conspicuous change which occurs. In pulps which have undergone a little further degeneration, the odontoblast layer becomes atrophied; fibrillar connective tissue becomes more abundant, coincidently with the diminution in the quantity of the cellular elements. Finally, the capillary system becomes obliterated by the occurrence of thrombosis in the larger vessels, the nerves undergo fatty degeneration, and the pulp becomes reduced to a shrivelled, unvascular, insensitive mass. These changes may go on without leading to actual putrefactive decomposition of the pulp, and are hence not attended by alveolar abscess; but a tooth in which the pulp has undergone senile atrophy is seldom fast in its socket.

The pulps of the teeth of some animals become eventually entirely converted into secondary dentine, but it would seem to be very generally the case that those teeth which exercise very active functions and last throughout the life of the creature retain their pulp in an active and vascular condition.

CEMENTUM.

The cement forms a coating of variable thickness over the roots of the teeth, sometimes, when the several roots are very close to another, or the cement is thickened by disease, uniting the several roots into one.

The cement is ordinarily said to be absent from the crowns of the teeth of man, the carnivora, &c., and to commence by a thin edge just at the neck of the tooth, overlapping the enamel to a slight extent; it is, in the healthy state, thickest in the interspaces between the roots of molar

or bicuspid teeth : it is, however, often thickened at the end of a root by a dental exostosis. In compound teeth, the cementum forms the connecting substance between the denticles (see the figures of the tooth of the Capybara, the Elephant, &c.), and, before the tooth has been subject to wear, forms a complete investment over the top of the crown. The cementum also covers the crowns of the complex-patterned crowns of the teeth of ruminants ; and, in

Fig. 52 ([1]).

my opinion, is present in a rudimentary condition upon the teeth of man, &c., as Nasmyth's membrane. The cementum is the most external of the dental tissues : a fact which necessarily follows from its being derived more or less directly from the tooth follicle.

Both physically and chemically, and also in respect of the manner of its development, the cementum is closely allied to bone. It consists of a laminated calcified matrix or basal substance, and lacunæ. Vascular canals corresponding to

([1]) Thick laminated cementum from the root of a human tooth.

the Haversian canals of bone, are met with, but it is only in thick cementum that they exist ; and, in man, perhaps in exostosis more often than in the thick healthy tissue.

The lamellæ of the cementum are thinner towards the neck of the tooth, being thickest at the apex of the root, but the number of the lamellæ is about the same in all parts of the tooth.

Soon after the completion of a tooth, there are but few lamellæ, and an adult has cementum far thicker than a

FIG. 53 ([1]).

child ; an aged person again having more than an adult. Very possibly it is to be regarded as growing at intervals through the life of the individual (Black).

The matrix is a calcified substance, which, when boiled yields gelatine, and if decalcified retains its form and structure : it is, in fact, practically identical with the matrix of bone. It is sometimes apparently structureless, at others finely granular, or interspersed with small globules.

The lacunæ of cementum share with those of bone the following characters : in dried sections they are irregular cavities, elongated in the direction of the lamellæ of the matrix, and furnished with a large number of processes. The processes of the lacunæ (known as canaliculi) are most

([1]) Lacuna of cementum which communicates with the terminations of the dentinal tubes.

abundantly given off at right angles to the lamellæ (see Fig. 52), and, again, in cementum, are more abundantly directed towards the exterior of the root than towards the dentine. The lacunæ of cementum differ from those of bone in being far more variable in size, in form, and in the excessive number and length of their canaliculi; in this latter respect the lacunæ of the cement of Cetacean teeth are very remarkable.

Many of the lacunæ in cementum are connected, by means of their canaliculi, with the terminations of the dentinal tubes (Fig. 53); they, by the same means, freely intercommunicate with one another, while others of their processes are directed towards the surface, which, however, in most instances, they do not appear to actually reach.

The lacunæ assume all sorts of peculiar forms, especially in the thicker portion of the cement.

Here and there lacunæ are to be found which are furnished with comparatively short processes, and are contained within well-defined contours. Sometimes such a line is to be seen surrounding a single lacuna, sometimes several lacunæ are enclosed within it; lacunæ so circumscribed are called "encapsuled lacunæ," and were first observed by Gerber in the cement of the teeth of the horse (they are specially abundant in the teeth of the solidungulata). By cautious disintegration of the cementum in acids these encapsuled lacunæ may be isolated; the immediate walls of the lacunæ and canaliculi, just as in bone, being composed of a material which has more power of resisting chemical re-agents than the rest of the matrix.

The encapsuled lacunæ are to be regarded as individual osteoblasts, or nests of osteoblasts, which have to some extent preserved their individuality during calcification.

In the fresh condition it appears probable that the lacunæ are filled up by soft matrix, which shrinks up, and so leaves them as cavities in dried sections. It can hardly as yet be

said that the question of the contents of lacunæ has been finally settled, though the researches of Bödecker and Heitzmann have gone far towards doing so.

According to them each lacuna contains a protoplasmic body, which they term the cement corpuscle, with a central nucleus.

This nucleus may be large and surrounded by but little protoplasm, or it may be small; or there may be many nuclei.

The cement corpuscles communicate freely with one another by offshoots, those of large size occupying the conspicuously visible canaliculi of the lacunæ, whilst the finer offshoots are believed by them to form a delicate network through the whole basis substance or matrix. The cement corpuscles near to the external surface give off numerous offshoots which communicate with protoplasmic bodies in the periosteum. By this means the cementum can remain alive even when the pulp of the tooth is dead, and thus the tooth be in no way a mere foreign body, dead and inert.

Like bone, cementum contains Sharpey's fibres; that is to say, rods running through it at right angles to its own lamination, and, as it were, perforating it. These are probably calcified bundles of connective tissue. And it is by the medium of these that the alveolo-dental periosteum adheres to the cementum.

Where the cementum is very thin, as, for instance, where it commences at the neck of a human tooth, it is to all appearance structureless, and does not contain any lacunæ, and therefore no protoplasmic bodies: nevertheless lacunæ may be sometimes found in thin cementum, as, for example, in that thin layer which invests the front of the enamel of the rodent-like tooth of a wombat.

The cementum at the neck is also devoid of lamellæ; it appears to be built up by direct ossification of osteoblasts, the prismatic shape of which may be traced in it: Bödecker

describes it as permeated by a fine but abundant network of soft living matter. The larger dentinal tubes fall short of the boundary line at the neck, but a fine protoplasmic network crosses it. Bödecker states that it has a covering of epithelial elements, like those of the gum.

The outermost layer of thick cementum is a glassy film, denser apparently than the subjacent portions, and quite devoid of lacunæ; on the surface it is slightly nodular, and might be described as built up of an infinite number of very minute and perfectly fused globules; this is, in fact, the youngest layer of cement, and is closely similar to that globular formation which characterizes dentine at an early stage of its development.

The cementum is very closely, indeed inseparably, connected with the dentine, through the medium of the "granular" layer of the latter; the fusion of the two tissues being so intimate, that it is often difficult to say precisely at what point the one may be said to have merged into the other. And in this region there is an abundant passage of protoplasmic filaments across from the one to the other.

Nasmyth's membrane.—Under the names of Nasmyth's membrane, enamel cuticle, or persistent dental capsule, a structure is described about which much difference of opinion has been, and indeed still is, expressed. Over the enamel of the crown of a human or other mammalian tooth, the crown of which is not coated by a thick layer of cementum, there is an exceedingly thin membrane, the existence of which can only be demonstrated by the use of acids, which cause it to become detached from the surface of the enamel. When thus isolated it is found to form a continuous transparent sheet, upon which, by staining with nitrate of silver, a reticulated pattern may be brought out, as though it were made up of epithelial cells. The inner surface of Nasmyth's membrane, is, however, pitted for the reception of the ends of the enamel prisms, which may have

something to do with this reticulate appearance. It is exceedingly thin, Kölliker attributing to it a thickness of only one twenty-thousandth of an inch, but, nevertheless, it is very indestructible, resisting the action of strong nitric or hydrochloric acid, and only swelling slightly when boiled in caustic potash. Notwithstanding, however, that it resists the action of chemicals, it is not so hard as the enamel, and

Fig. 54 (1).

becomes worn off tolerably speedily, so that to see it well a young and unworn tooth should be selected.

Observations upon the presence or absence of Nasmyth's membrane in fish and reptiles are very much needed; my own recent investigations upon the development of the teeth in these classes make me doubt whether the *à priori* conclusion of Waldeyer, who believes that the cuticle will be found on all teeth, is not based upon an interpretation of its nature which is incorrect.

The observation of Professor Huxley, who believed that

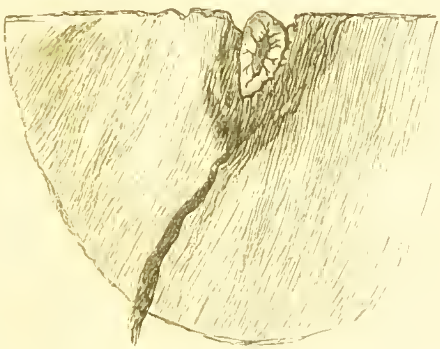
(1) From a section of a bicuspid tooth in which the cementum, *c*, is continued over the outside of the enamel, *a*; the dentine is indicated by the letter *b*.

he found it upon the teeth of the frog, &c., may be susceptible of another explanation, to which I shall have to recur, merely premising here that its presence is only certain in Primates, Carnivora, and Insectivora.

The singular power of resistance to re-agents which characterises it proves nothing more than that it is a tissue, imperfectly calcified, on the border-land of calcification, so to speak, since similarly resistant structures are to be found lining the Haversian canals, the dentinal tubes, the surface of developing enamel, the lacunæ, &c.

In my father's opinion (Dental Surgery, 1859) it is to be

FIG. 55 (1).



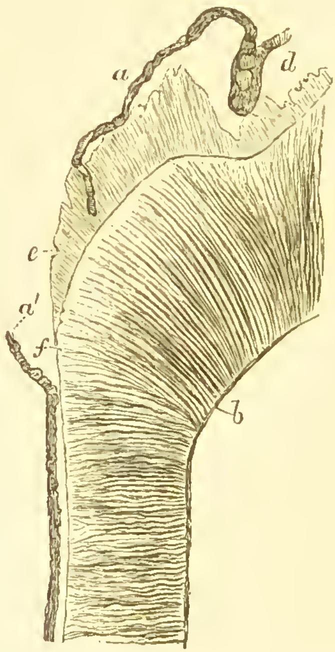
regarded as a thin covering of cementum, and I have given additional evidence in support of the view in a paper referred to already in the list of works which heads this chapter.

It now and then happens that the cementum upon a more or less abnormal tooth, instead of ceasing at the neck, is continued up over the exterior of the enamel. This occurs less uncommonly than is generally imagined, and the accompanying figure represents a portion of the crown of such a tooth.

(1) Encapsuled lacuna occupying a pit in the enamel.

If the section be made of the grinding surfaces of such teeth as present rather deep fissures in these situations, well marked and unmistakeable lacunal cells, or encapsuled lacunæ, will be met with with considerable frequency. Now and then an encapsuled lacuna may be found occupying a

FIG. 56 (1).



shallow depression in the enamel which it just fits, but more commonly a dozen or more are crowded together in a pit in the enamel, where they are usually stained of a brownish colour. The occurrence of lacunæ in these situations is far from rare: my father's collection contains more than a dozen good examples of them in these positions.

Nasmyth's membrane, thin though it is over the exterior

(1) Nasmyth's membrane, set free by the partial solution of the enamel. *a*. Nasmyth's membrane. *b*. Dentine. *d*. Mass occupying a pit in the enamel. *c*. Enamel. *a'*. Torn end of Nasmyth's membrane.

of the enamel, is thickened when it covers over a pit or fissure, and when isolated by an acid is seen to have entirely filled up such spots. (Fig. 56.)

In these places, then, where the encapsuled lacunæ are to be found, Nasmyth's membrane also exists, a fact which alone would lend some probability to the view that it is cementum.

The general absence of lacunæ in Nasmyth's membrane is due to the fact that it is not thick enough to contain them; just as the thinnest layers of unquestionable cementum also are without lacunæ.

In sections of an unworn bicuspid which was treated with acid subsequently to its having been ground thin and placed upon the slide, I have several times been fortunate enough to get a view of the membrane *in situ;* it then appears to be continuous with an exterior layer of cementum, which becomes a little discoloured by the acid employed to detach Nasmyth's membrane from the enamel. I am therefore inclined to regard it as young and incomplete cementum, and to consider it as representing (upon the human tooth) the thick cementum which covers the crowns of the teeth of Herbivora; and I am very glad to learn from my friend Dr. Magitot, who has made many as yet unpublished researches upon this subject, that he entirely concurs in this view, which has also the support of Professor Wedl.

The evidence offered that Nasmyth's membrane is cementum, although strong, does not amount to absolute proof; it is therefore desirable to briefly recapitulate the other explanations of its nature which have been offered.

Nasmyth, who first called attention to its existence, regarded it as "persistent dental capsule;" a view of its nature not very materially differing from that advocated in these pages.

Professor Huxley described it as being identical with the membrana performativa; that is to say, with a membrane which covered the dentine papilla prior to the occurrence of calcification, and which afterwards came to intervene between the formed enamel and the enamel organ. The objections to the acceptance of this

view of its nature are so inextricably wrapped up with other objections to Professor Huxley's theory of the development of the teeth, that they cannot profitably be detailed in this place: it will suffice to say, that evidence and the weight of authority alike point to there being no such true membrane as this membrana performativa in the place in question.

Waldeyer holds that it (*i.e.*, Nasmyth's membrane) is a product of a part of the enamel organ. After the completion of the formation of the enamel he believes that the cells of the external epithelium of the enamel organ become applied to the surface of the enamel and there *cornified;* in this way he accounts for its resistance to reagents, and for its peculiar smell when it is burnt.

Its extreme thinness, so far as it goes, is an objection to this supposition: a more weighty argument against it is the absence of analogy for such a peculiar change, by which one portion of the same organ is calcified, and the rest cornified; and again, what becomes of these cells in those teeth in which cementum is deposited in bulk over the surface of the enamel? According to the statement of Dr. Magitot, the layer of cells in question (external epithelium of the enamel organ) is atrophied before the time of the completion of the enamel; a fact which, if confirmed, is fatal to Waldeyer's explanation. And Dr. Magitot, in his most recent paper on the subject (Journal de l'Anatomie, &c., 1881), gives his adherence to the view that it is cementum.

Kölliker, who dissents strongly from the views of Waldeyer, and admits some uncertainty as to its nature, provisionally regards it as a continuous and structureless layer furnished by the enamel cells after their work of forming the fibrous enamel was complete; a sort of varnish over the surface, as it were.

This would not account for the occurrence of lacunæ in it.

THE GUM.

The gum is continuous with the mucous membrane of the inside of the lips, of the floor of the mouth, and of the palate, and differs from it principally by its greater density. Its hardness is in part due to the abundant tendinous fasciculi which it itself contains, in part to its being closely bound down to the bone by the blending of the dense fibrous fasciculi of the periosteum with its own. The fasciculi springing from the periosteum spread out in fan-like shape as they approach the epithelial surface. There is thus no

very sharp line of demareation between the gum and the periosteum when these are seen in seetion *in situ.*

The gum is beset with rather large, broad-based papillæ, whieh are sometimes single, sometimes eompound; the epithelium is eomposed of laminæ of tesselated eells, mueh flattened near to the surface; but eylindrieal eells form the deepest layer of the epithelium, the rete Malpighi.

Small round aggregations of pavement epithelium are met with at a little depth, or even bedded in the surfaee; these, the "glands" of Serres, have no known signifieance. In the neighbourhood of developing tooth-saes epithelial aggregations of similar appearanee are to be met with, and in sueh spots are remains of the neek of the enamel organ (ef. page 145), whieh has undergone this eurious ehange subsequently to the eompletion of its original funetion. The gums are rieh in vessels, but remarkably seantily supplied with nerves.

At the neeks of the teeth the gum beeomes eontinuous with the periosteum of the internal surfaee of the alveoli into whieh it passes without any line of demareation.

The Alveolo-Dental Membrane.

The Alveolo-dental Periosteum, or Root membrane, is a eonnective tissue of moderate density, devoid of elastie fibres, and richly supplied with nerves and vessels.

It is thieker near to the neek of the tooth, where it passes by imperceptible gradations into the gum and periosteum of the alveolar process, and near to the apex of the root. The general direction of the fibres is transverse; that is to say, they run across from the alveolus to the cementum, without break of continuity, as do also many capillary vessels; a mere inspeetion of the conneetive tissue bundles, as seen in a transverse seetion of a deealcified tooth in its

socket, will suffice to demonstrate that there is but a single "membrane," and that no such thing as a membrane proper to the root and another proper to the alveolus can be distinguished; and the study of its development alike proves that the soft tissue investing the root, and that lining the socket, are one and the same thing: that there is but one "membrane," namely, the alveolo-dental periosteum.

At that part which is nearest to the bone the fibres are grouped together into conspicuous bundles; it is, in fact, much like any ordinary fibrous membrane. On its inner aspect, where it becomes continuous with the cementum, it consists of a fine network of interlacing bands, many of which lose themselves in the surface of the cementum.

But although there is a marked difference in histological character between the extreme parts of the membrane, yet the markedly fibrous elements of the outer blend and pass insensibly into the bands of the fine network of the inner part, and there is no break of continuity whatever.

The actual attachment, both to the cementum and to the bone, takes place by means of the connective tissue fibres, which pass right into the hard structures, which they traverse for some distance, and in this situation are known as Sharpey's fibres.

They pass through all the lamellæ of the cementum, and there are appearances of shrinkage in dry preparations which would lead to the inference that they were not very fully calcified; in some portions of the cementum it seems to be almost composed of them, as at the neck of a tooth (Black). This writer states that they may be especially clearly seen in the pig, and that "they are the principal fibres of the peridental membrane included in the cementum in its growth, and furnish the means of making firm hold of the peridental membrane upon the root of the tooth. They are white connective tissue fibres, the ends of which are included in the matrix of the cementum sufficiently to make

them apparent when the lime salts are removed, but when both are calcified, they cannot be demonstrated except in cases where there is imperfect calcification of the fibres, as has been mentioned above."

The thickness of the membrane appears to undergo a diminution with age, by calcification encroaching upon it from both the side of the bone and of the cementum.

Malassez ("Archiv de Physiologie," 1885) urges that an ordinary periosteum in this situation would be too tender for the purposes of mastication, and that as it is not a mere enveloping membrane, but is composed of fibrous bundles, which serve to sling the tooth in its place, it should be called the alveolodental ligament; he further compares it with the fibrous bands which in some fishes serve to tie the tooth down to the bone where no tooth sockets exist, and holds that it is strictly homologous with these. Ranvier also points out that there is no isolable membrane such as there is on a long bone, and compares the alveolar cavity and its contents to a very large medullary space.

At the surface of the cementum it is more richly cellular, and here occur abundantly large soft nucleated plasm masses, which are the osteoblasts concerned in making cementum, and which by their offshoots communicate with plasm masses imprisoned within the cementum.

I have rarely seen the fibres, whether in longitudinal or in transverse sections, pass straight in the shortest possible line from the bone to the cementum, but they invariably pursue an oblique course, which probably serves to allow for slight mobility of the tooth without the fibres being stretched or torn.

The blood vessels are most abundant in membrane midway between the bone and the cementum, or rather nearer to the latter; but close to it there is a rich capillary plexus without large vessels. A good many of the arteries enter the apical region, and break up to go, partly to the tooth pulp

and partly to the periosteum, some of them reaching right from the apex to the gum; they anastomose freely with vessels in the bone and with those of the gum, so that the blood supply is not easily interfered with.

Fig. 57 (1).

The vascular supply of the root membrane is, according to Wedl, derived from three sources; the gums, the vessels of the bone, and the vessels destined for the pulp of the tooth, the last being the most important.

(1) Portion of the side of the root of a tooth, the gum and alveolo-dental membrane, and the edge of the bone of the alveolus.

A band of fibres is seen passing over the surface of the alveolus and dividing, some to pass upwards into the gum, others to pass more directly across to the cementum. Numerous orifices of vessels cut across transversely are seen between the tooth and the bone.

The nerve supply also is largely derived from the dental nerves running to the dental pulps; other filaments come from the inter-alveolar canals (canals in the bone, containing nerves and vessels, which are situated in the septa separating the alveoli of contiguous teeth).

It should be borne in mind that the tooth pulp and the tissue which becomes the root membrane have sprung from the same source, and were once continuous over the whole base of the pulp. A recognition of this fact makes it easier to realise how it comes about that their vascular and nervous supplies are so nearly identical.

Several observers have laid stress upon the occurrence of cells upon the surface of the cementum, deep down in the tooth sockets, which are unlike osteoblasts, but are very much like epithelial cells. It is claimed by von Brunn that the enamel organ goes far below the region where enamel is to be formed, and that it is in fact co-extensive with the dentine, thus necessarily intervening between the dentine and the cement-forming tissue; he describes the connective tissue bundles as growing through it to attach themselves to the dentine, and thus cutting up the remains of this enamel organ into small isolated areas, which are to be found here and there in the adult alveolo-dental periosteum.

Dr. Black describes another type of cells which he believes to be lymph cells lining lymph canals; these are always found close to cementum. He believes also, as corroborative of this view, that he has been able to trace pus infiltration along these chains of cells.

The human tooth is, accepting as correct the researches of Bödecker, which appear in every way deserving of credence, connected with the living organism very intimately, even though its special tissues are extra-vascular.

For blood vessels and nerves enter the tooth pulp in abundance; the dentine is organically connected with the

pulp by the dentinal fibrils; these are connected with the soft cement corpuscles, which again are brought by their processes into intimate relation with similar bodies in the highly vascular periosteum.

So that between pulp inside, and periosteum outside, there is a continuous chain of living plasm.

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CHAPTER IV.

THE DEVELOPMENT OF THE TEETH.

The development of the teeth is a process which, while subject to modifications in the different groups of vertebrates, retains nevertheless in all certain essential characters, so that it becomes possible to embody its main features in a general account.

Prior to the commencement of any calcification there is always a special disposition of the soft tissues at the spot where a tooth is destined to be formed; and the name of "tooth germ" is given to those portions of the soft tissue which are thus specially arranged. All, or a part only, of the soft structures making up a tooth germ, become converted into the dental tissues by a deposition of salts of lime within their own substance, so that an actual conversion of at least some portions of the tooth germ into tooth takes place. The tooth is not secreted or excreted by the tooth germ, but an actual metamorphosis of the latter takes place. The details of this conversion can be better discussed at a later page; for the present it will suffice to say that the three principal tissues, namely, dentine, enamel, and cementum are formed from distinct parts of the tooth germ, and that we are hence accustomed to speak of the enamel germ and the dentine germ; the existence of a special cement germ is asserted by Magitot, but as yet his descriptions await confirmation.

In many anatomical works the process of tooth development used and may sometimes still be found to be divided

into periods, under the names of "papillary," "follicular," and "eruptive" stages.

These stages are based upon a false conception, upon theories now known to be incorrect, and may advantageously be absolutely abandoned. The account of the development of the teeth given in the following pages (based in the case of man and mammals upon the researches of Kölliker, Thiersch, and Waldeyer; in the case of reptiles and fishes, upon those of Huxley and Santi Sirena, and upon Hertwig's and my own), will be found to differ from the older accounts published by a deservedly great authority, Professor Owen. Modern methods of research have disclosed facts heretofore not demonstrable; yet twenty years ago Professor Huxley demonstrated in a remarkable paper the incorrectness of certain of the theories then promulgated. Of the general accuracy of the following description I am however fully satisfied, and most of the facts may be easily verified by any one desirous of so doing.

True tooth germs are not formed quite upon the surface (1), but are always situated at a little distance beneath it, in some creatures ultimately coming to lie at a considerable depth. Every known tooth germ consists in the first instance of two portions, and two only, the enamel germ and the dentine germ; and these are derived from distinct sources, the former being a special development from the epithelium of the mouth, the latter from the more deeply lying parts of the mucous membrane. Other things, such as a tooth capsule, may be subsequently and secondarily formed, but in the first instance, every tooth germ consists of an enamel germ and a dentine germ only, and the simplest tooth germs never develop any additional parts. The existence of an enamel organ in an early stage is therefore perfectly independent of any subsequent formation of

(1) The placoid scales of embryonic sharks are, however, formed on the surface, and the "germs" covered in by epithelium only (Hertwig).

enamel by its own conversion into a calcified tissue, for I have shown that it is to bo found in the germs of teeth which have no enamel; in fact, in all known tooth germs whatever.

That part of the tooth germ destined to become dentino is often called the dentine papilla, having acquired this name from its papilliform shape; and in a certain sense it is true that the enamel organ is the epithelium of the dentine papilla. Yet, although not absolutely untrue, such an expression might mislead by implying that the enamel organ is a secondary development, whereas its appearance is contemporaneous with, if not antecedent to, that of the dentine germ. The most general account that I am able to give of the process is, that the deeper layer of the oral epithelium sends down into the subjacent tissue a process, the shape and structure of which is, in most animals, distinguishable and characteristic before the dentine germ has taken any definite form. This process enlarges at its end, and, as seen in section, becomes divaricated, so that it bears some resemblance to an inverted letter Y; or it might more truthfully be compared to a bell jar with a handle; this constitutes the early stage of an enamel germ (see Fig. 65), while beneath it in the mucous tissue, the dentine germ assumes its papilliform shape. The details of the process varying in different creatures, I will at once proceed to the description of the development of teeth in the various groups.

In **Elasmobranch Fishes.**—If a transverse section through the jaw of a dog-fish (Scyllium canicula) be examined, we shall find that the forming teeth lie upon the inside of the semi-ossified jaw-bones, the youngest being at the bottom (Fig. 58); progressing upwards, each tooth is more fully calcified till, on passing over the border of the jaw, we come to those teeth whose period of greatest usefulness is passed and which are about to be cast off in the

course of that slow rotation of the whole tooth-bearing mucous membrane over the border of the jaw, which is constantly going on.

In the section figured there are four teeth advanced in calcification, while beneath them are four tooth germs in earlier stages; of the former two only are fully protruded through the epithelium, the third being in part covered in; the remaining teeth are altogether beneath the surface of the epithelium, and therefore shut off from the cavity of the mouth, if the soft parts be all *in situ.*

All the teeth not fully calcified are covered in and protected by a reflexion upwards of the mucous membrane (*c* in the figure), which serves to protect them during their calcification.

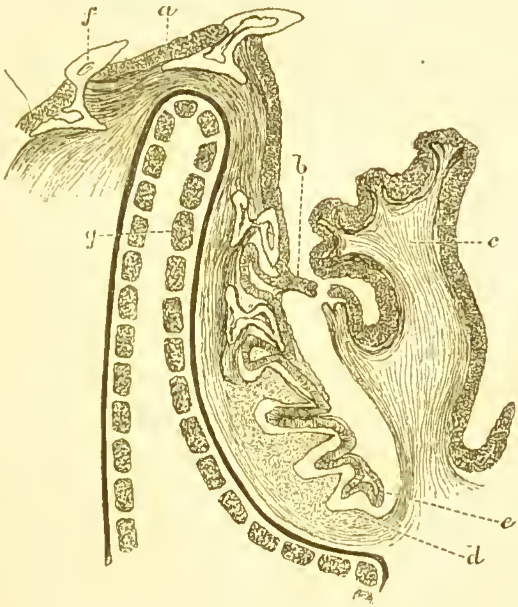
But although this may be termed a fold reflected upwards, it is not, as was supposed by Professor Owen, a free flap, detached from the opposite surface on which the teeth are developing; there is no deep open fissure or pouch running round inside the jaw, as would in that case exist, and the epithelium does not pass down on the one side to the bottom of such fissure, and then ascend upon the other as a distinct layer. Although the fold is very easily torn away from the tooth germs which it covers in, yet in the natural condition it is attached, and there is no breach of surface; the epithelium passing across from the jaw to cover it is well seen in the figure, in which the epithelial layer is represented as broken just at the point (between the third and fourth teeth) where it leaves the jaw to cross over on to the surface of the flap.

The conditions met with in the Elasmobranch fishes are peculiarly favourable for the determination of the homologies of the several parts of the tooth germ and of the formed tooth (1). At the base of the jaw, where the youngest tooth germs are to be found, the tissue whence the dentine

(1) Compare the description of the placoid dermal spine (page 2).

papillæ arise blends insensibly with that making up the substance of the thecal fold on the one hand, and on the

FIG. 58 ([1]).



other, with that clothing the convexity of the jaw and giving attachment to the teeth.

No sharp line of demarcation at any time marks off the base of the dentine papilla from the tissue which surrounds it, and from which it springs up, as would be the case in mammalian or reptilian tooth germs; all that can be said is, that the dentine germs are cellular, the cells being large and rounded, while in the rest of the mucous membrane the fibrillar elements preponderate, so that it passes by

([1]) Transverse section of lower jaw of a Dog-fish. *a.* Oral epithelium. *b.* Oral epithelium passing on to flap. *c.* Protecting flap of mucous membrane (thecal fold). *d.* Youngest dentine pulp. *e.* Youngest enamel organ. *f.* Tooth about to be shed. *g.* Calcified crust of jaw.

imperceptible gradations into the densely fibrous gum, found on the exposed border of the jaw.

The dentine germs, and consequently the dentine, are indisputably derived from the connective tissue of the mucous membrane immediately subjacent to the epithelium, nor can it be doubted that the enamel organs are simply the modified epithelium of that same mucous membrane.

Of course there is nothing new in this conclusion, which had been already arrived at by the study of other creatures, but the sharks happen to demonstrate it with more clearness than those other animals in whom the original nature of the process is more or less masked by the introduction of further complexities.

Hence it is worth while to study carefully the relations of the epithelium constituting the enamel organs with that of the surface of the mouth. As has been already mentioned, in the normal condition of the part there is no deep fissure on the inner side of the jaw, but the epithelium passes across (from the interspace between the third and fourth teeth in the figure) on to the protecting fold of mucous membrane (*c* in fig.). But although the epithelium is reflected across on to the thecal fold, it is also continued downwards along the inner side of the developing teeth and tooth germs, giving to each a complete investment, and filling up the whole interval between the tooth germ and the thecal fold. The epithelium in this situation does not, then, consist simply of one layer going down on the one side and covering the tooth germs, and then reflected up at the bottom to coat the inner side of the thecal fold, but it is so arranged as to have relation only to the tooth germs; it is termed "enamel organs" because over the tooth germs these epithelial cells assume a marked columnar character, and are very different in appearance from the epithelium elsewhere.

The terminal portion of this epithelium, or, in other words, the youngest enamel germ, forms a bell-like cap over the eminence of mucous membrane connective tissue which constitutes the earliest dentine germ, and in section is of the form shown in the figure. The surface next to the dentine papilla consists of elongated columnar cells, with nuclei near to their attached extremities, while the rest of its substance is made up of much smaller cells, some of which have inosculating processes, so that they constitute a sort of finely cellular connective tissue, very different in appearance from anything met with in mammalian enamel organs. It is sufficiently consistent to keep up the continuity of all the enamel organs, even when displaced in cutting sections, so that the whole might be described as forming one composite enamel organ. The columnar cells already alluded to invest the whole surface which is directed towards the forming teeth, but they atrophy somewhat in the interspaces of the tooth germs.

Before proceeding further in the description of the development of the tooth germs, it will be well to refer to a somewhat earlier stage in the growth of the Dog-fish, in which the relation subsisting between the teeth and the dermal spines is still well seen.

On the lower jaw of the young dog-fish there is no lip; hence, as is seen in the figure, the spines which clothe the skin come close to the dentigerous surface of the jaw.

Although there are differences in form and size, a glance at the figure will demonstrate the homological identity of the teeth and the dermal spines. As the dog-fish increases in size, this continuity of the teeth with the dermal spines on the outside of the head becomes interrupted by an extension of the skin to form a lip; this happens earlier in the upper jaw than in the lower, and at first the spines are continued over the edge and the inside of the newly formed lip—from these situations, however, they soon disappear. In structure,

the teeth and the dermal spines are, in many species, very closely similar; the latter are, however, much less often shed and reproduced, so that it is less easy to find them in all stages of their growth; I believe, however,' that they follow a course essentially similar to that of the teeth.

It is stated by Gegenbaur that in Selachia the mucous

Fig. 59 (1).

membrane of the mouth is clothed with spines of a structure similar to that of the teeth, and that these spines are often limited to particular regions, extending back as far as the pharynx—these same regions in Ganoids and Osseous fishes being occupied by conspicuous teeth; and Hertwig has shown that the dermal spines are developed in a manner precisely analogous to that described in the teeth, save that the germs are even less specialised.

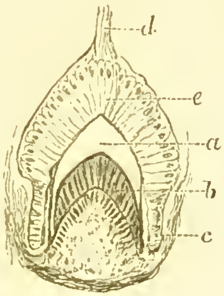
In Teleostei or Osseous Fishes.—In passing from the consideration of the development of the tooth germs of Elasmobranch to those of Osseous fishes, the first difference to be noted is this: whereas in the former each tooth germ was, so far as the enamel germ is concerned, derived from that

(1) Section of lower jaw of young Dog-fish, showing the continuity of the dermal spines of the skin under the jaw, with the teeth which lie above and over its end.

of the next older tooth, in the latter each enamel germ often arises independently and, as it were, *de novo*. At all events, so far as my own investigations go, no connection has been traced between the germs of teeth of different ages; but Heincke says that in the Pike new enamel organs may be derived from older ones.

This independent origin of an indefinite number of teeth,

FIG. 60 ([1]).



having no relation to their predecessors, is only certainly known to occur in the osseous fish: of the development of the teeth of Ganoid fish nothing is known.

The oral epithelium, which varies much in its thickness and in other characters in different fishes, sends down a process which goes to form an enamel organ, whilst a dentine papilla in rising up to meet it, comes to be invested by it as with a cap. The after-history of the process depends much on the character of tooth which is to be formed. If no enamel, or but a rudimentary coat of enamel, is to be formed, the cells of the enamel organ remain small and insignificant, as in the mackerel. If, on the other hand, a partial investment of enamel is found upon the perfected tooth, such for instance, as the little enamel tips upon the teeth of the

([1]) Tooth-germ of an eel. *d.* Neck of enamel organ. *e.* Enamel cells. *a.* Cap of enamel. *b.* Cap of dentine. *c.* Rudimentary enamel cells opposite to that part of the dentine germ where no enamel will be formed.

eel (see Fig. 93), then the after-development of the enamel organ is very instructive.

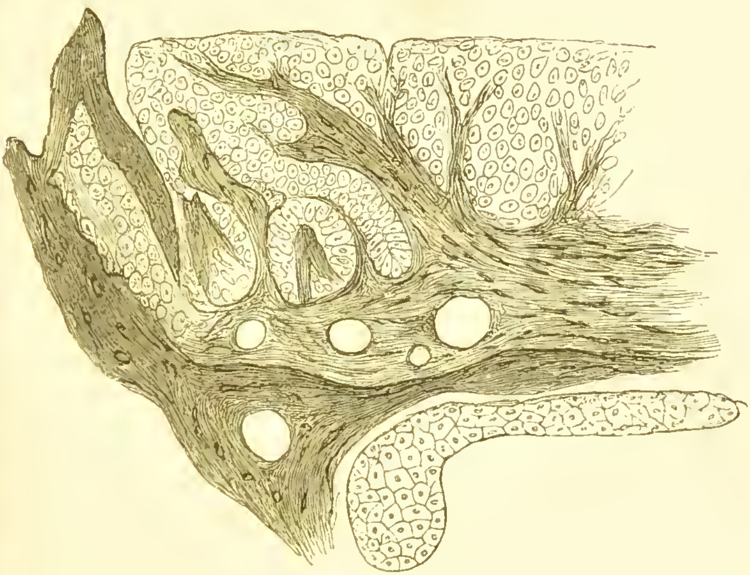
Opposite to the apex of the dentine papilla, where the enamel cap is to be, the cells of the enamel organ attain to a very considerable size, measuring about $\frac{1}{400}$ of an inch in length; below this the investing cap of enamel organ does not cease, but it is continued in a sort of rudimentary condition. Thus, although the enamel organ invests the whole length of the dentine papilla, its cells only attain to any considerable size opposite to the point where the enamel is to be formed. The knowledge of this fact often enables an observer to say, from an inspection of the tooth germ, whether it is probable that the perfected tooth will be coated with enamel or not. In any case an enamel organ will be there, but if no enamel is to be formed, the individual cells do not attain to any considerable degree of differentiation from the epithelium elsewhere; in other words, the whole enamel organ will partake of the character of the lower portion of that represented in the figure of the tooth germ of the eel.

Although of course there are many differences of detail arising from the very various situations in which teeth are developed in fish, so great uniformity pervades all which I have examined, that we may at once pass on to the consideration of the development of the teeth of reptiles, merely adding that it is not altogether true to say that the teeth of fish in their development exemplify transitory stages in the development of mammalian teeth.

In Reptiles, so far as the appearances presented by the individual germs go, there are few differences worthy of note to be found by which they are distinguishable from those of either fish or mammals. The enamel organ is derived from the oral epithelium, and the dentine organ from the submucous tissue in a very similar manner; nevertheless, there are points in the relation which

the successional tooth germs bear to one another, and to the teeth already *in situ*, which are of some little interest. The constant succession of new teeth met with amongst almost all reptiles renders it easy to obtain sections showing the teeth in all stages of growth : upon the inner side of the jaw there will be found a region occupied by these forming teeth

FIG. 61 (1).



and by nothing else, which may be called "area of tooth development ;" this is bounded on the one side by the bone and teeth which it carries, and on the other by a more or less sharply defined wall of fibrous connective tissue. In the newt for example (Fig. 61), to the left of the tooth in use are seen four tooth sacs, in serial order, the youngest being nearest to the median line of the mouth. As the sacs increase in size they appear to undergo a sort of migration

(1) Section of upper jaw of *Triton cristatus* (newt). To the inner side of the tooth attached to the bone are three younger tooth germs.

towards the edge of the jaw, while simultaneously new ones are constantly being developed beyond them. In the newt, the ingrowth of the epithelium is obviously the first step apparent; this ingrowth of a process of epithelium takes place in close relation with the "neck" of an older enamel organ (*i.e.*, the contracted band of epithelium which remains for some time connecting the new enamel organ with the epithelium whence it was derived). New enamel organs are therefore not derived directly from the epithelium of the surface, but from the necks of the enamel organs of their predecessors.

In the newt, the developing teeth spread out for a considerable distance towards the palate, and thus, being free from crowding, the relations of the enamel organs of three or four successional teeth of serial ages may be studied in a single section; and the arrangement so disclosed may be advantageously compared with that seen in the dog-fish (see Fig. 58).

The tooth sac of the newt is a good example of the simplest form of tooth sac, consisting solely of an enamel organ and a dentine germ, without any especial investment. The "sac" is wholly cellular, and on pressure breaks up, leaving nothing but cells behind it. The cells of the enamel organ are large, and resemble those of the eel; the teeth of newts have a partial enamel tip, like those of the fish referred to, but differing from them in being bifurcated, as is very early indicated by the configuration of the enamel organ.

In the frog there is a peculiarity in the manner in which the two jaws meet, the edentulous lower jaw, which has no lip, passing altogether inside the upper jaw and its supported teeth, and so confining the area of tooth development within very narrow limits. Consequently I have been unable to satisfy myself whether the new tooth germs, or rather their enamel organs, are derived from those of their predecessors, or spring up *de novo;* analogy would indicate

the former, but appearances tend towards the latter supposition.

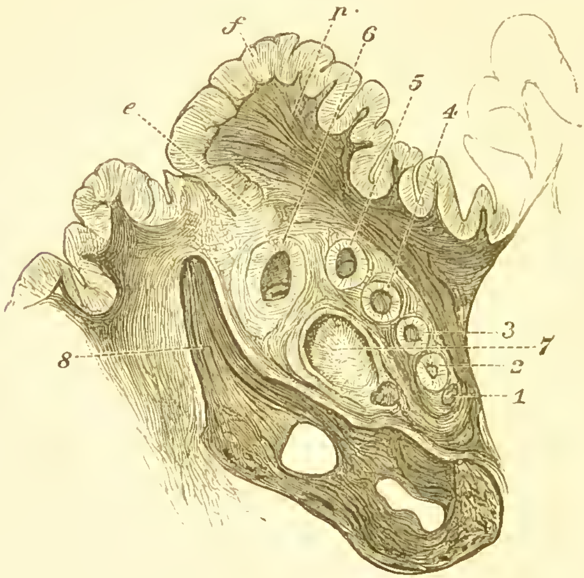
In the lizards the new tooth germs are formed a very long way beneath the surface, so that the neck of the enamel organ becomes enormously elongated, for the dentine papilla is, just as in the newt, situated at first quite at the level of the floor of the area of tooth development. The teeth of the lizards have a more complete investment of enamel, hence the enamel cells are developed upon the side of the dentine germ to a much lower point than in the newt. The germs also acquire an adventitious capsule, mainly derived from the condensation of the connective tissue around them, which is pushed out of the way as they grow larger. The further progress of the tooth germ being identical with that of mammalia, its description may be for the present deferred.

In ophidian reptiles (snakes) several peculiarities are met with which are very characteristic of the order. A snake's method of swallowing its food would seem to render the renewal of its teeth frequently necessary; although I do not know of any data by which the probable durability of an individual tooth could be estimated, the large number of teeth which are developing in reserve, all destined to succeed to the same spot upon the jaws, would indicate that it is short.

I have seen as many as seven successional teeth in a single section, and their arrangement, particularly in the lower jaw, which undergoes great displacement while food is being swallowed, is very peculiar. The numerous successional tooth sacs, instead of being spread out side by side, as in the newt, are placed almost vertically, and in a direction parallel with the surface of the jaw-bone; they are, moreover, contained in a sort of general investment of connective tissue; a species of bag to keep them from displacement during the expansion of the mouth.

The inward growing proeess of oral epithelium enters this ease of tooth saes at its top; and may be eaught sight of here and there as its prolongations wind their way by the sides of the tooth saes to the bottom of the area. Here the familiar proeess of the formation of an enamel organ and

FIG. 62 (1).



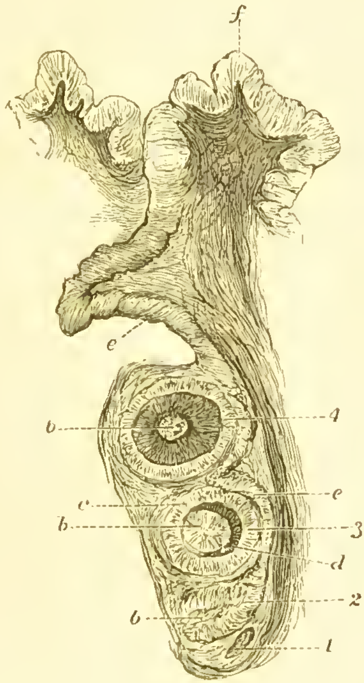
dentine papilla may be observed, in no essential point differing from that which is to be seen in other animals.

That the derivation of eaeh enamel organ is from a part of that of its predeeessor is very obvious; the dentine organs are formed in relation with the enamel germs, but apparently independently ofone another.

(1) Transverse section of the lower jaw of common English Snake. *c.* Inward dipping process of epithelium. *f.* Oral epithelium. 1, 2, 3, &c. Tooth germs of various ages. S. Tooth in place, cut somewhat obliquely, so that its tip apparently falls short of its surface, and does not project above the mucous membrane.

As the tooth sacs attain considerable dimensions, a curious alteration in position takes place; instead of preserving a vertical position, they become recumbent, so that the forming tooth lies more or less parallel with the long axis of the

FIG. 63 (1).



jaw. The utility of such an arrangement is obvious: were the tooth to remain erect after it has attained to some little length, its point would probably be forced through the mucous membrane when the mouth was put upon the stretch; but while it lies nearly parallel with the jaw no such accident can occur.

The tooth does not resume the upright position until it finally moves into its place upon the summit of the bone.

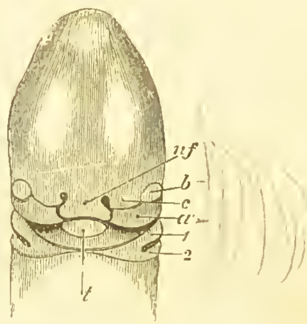
(1) Developing teeth of a Snake. *f.* Oral epithelium. *c.* Neck of the enamel organs. *b.* Dentine pulp. *c.* Enamel cells. *d.* Dentine. 1, 2. Very young germs. 3, 4. Older germs.

As has already been mentioned, there is a well-developed enamel organ with large enamel cells: from these a thin layer of enamel is formed, and thus the thin exterior layer upon the teeth of snakes is true enamel, and not, as has been usually supposed, cementum.

Many points in the development of the teeth of reptiles I have passed over very briefly for the want of space; a more full account of my observations will be found in the Philosophical Transactions for 1875.

In Mammalia the earliest changes which will ultimately

FIG. 64 [1].



result in the formation of a tooth are traceable at a very early period; before ossification has set in, the lower jaw consisting solely of Meckel's cartilage imbedded in embryonic tissue, and the lateral processes which become the upper maxillary bones having but just reached as far as the median process which constitutes the intermaxillary bone. That is to say, about the fortieth or forty-fifth day (in the human subject), in the situation corresponding to the future alveolar border, there appears a slight rounded depression, extending the whole length of the jaw, it and its elevated borders being

[1] Embyro at end of fifth week, after Carpenter. 1, 2. First two visceral arches. *a.* Superior maxillary process. *t.* Tongue. *b.* Eye. *c.* Lateral nasofrontal process. *nf.* Nasofrontal process.

formed by an increase in the thickness of the layer of epithelial cells; while in transverse sections the proliferation of epithelial cells is found to have been even more energetic in a direction downwards into the substance of the jaw than it is upwards, so that a *cul-de-sac* of epithelium dips into the embryonic sub-mucous tissue. [1]

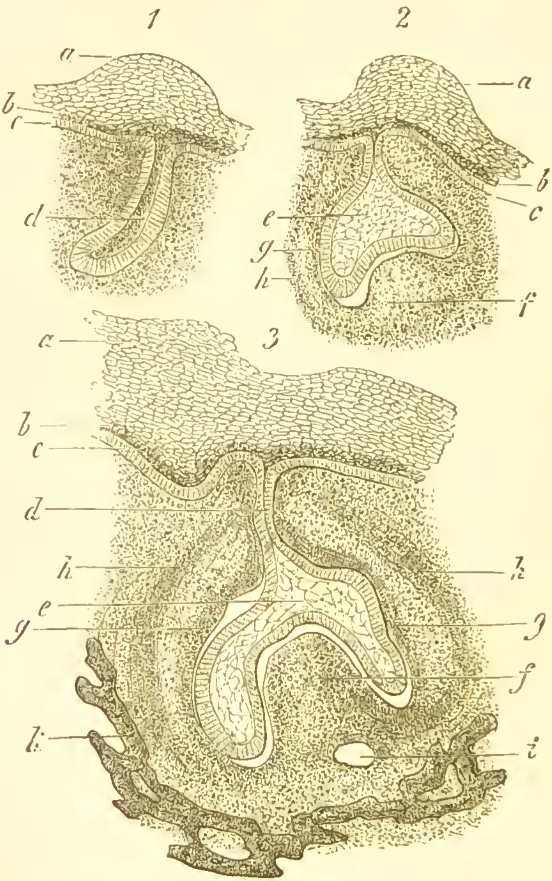
In a certain sense, then, there is a dental groove, but it is not the same thing as that described as such in the text-books, and it is therefore better to abstain from applying that or any other name to the shallow furrow of which we are now speaking, which is almost filled up with spherical or flattened cells, the deepest layer being, however, columnar cells. From the bottom, or the side near the bottom of the depression, an inflection of epithelial cells takes origin; it does not dip downwards vertically, but inclines inwards. This narrow inflection of epithelium, which in section closely resembles a tubular gland, constitutes the rudiment of the future enamel organ; a proliferation of the cells at its deepest extremity speedily takes place, so that it expands, attaining somewhat the form of a Florence flask (Fig. 65). It should, however, be noted, that while the inflection of epithelium takes place around the entire circumference of the jaw, so that that which appears in sections like a tubular gland is really a continuous sheet or lamina of epithelium, the dilatations of its extremity, which I have compared to a Florence flask, occur only at the several points where teeth will ultimately be developed.

The cells upon the periphery are columnar, polygonal cells occupying the central area of the enlargement. Very

[1] The epithelium having been removed by maceration or by keeping a specimen in dilute spirit, a groove would result, and this is probably what was seen and described by Goodsir as the "primitive dental groove": but, as the student will gather from the text, there is at no time any such thing as a deep open groove like that described by him, unless it results from maceration and consequent partial destruction of the specimen.

soon the terminal enlargement, as it grows more deeply into the jaw, alters in form; its base becomes flattened,

Fig. 65 ([1]).



and the borders of the base grow down more rapidly than the centre, so that its deepest portion presents a concavity

([1]) Three stages in the development of a mammalian tooth germ (after Frey). *a*. Oral epithelium heaped up over germ. *b*. Younger epithelial cells. *c*. Deep layer of cells, or rete Malpighi. *d*. Inflection of epithelium for enamel germ. *e*. Stellate reticulum. *f*. Dentine germ. *g*. Inner portion of future tooth sac. *h*. Outer portion of future tooth sac. *i*. Vessels cut across. *k*. Bone of jaw.

looking downwards; it might be compared to a bell, suspended from above by the thin cord of epithelium which still connects it with the epithelium of the surface, or it might in section be described as crescentic, the horns of the crescent being long, and looking downwards. Coincident with the assumption of this form by the enamel germ, is the appearance of the dentine germ; but it will facilitate the description of the process to pursue a little farther the development of the enamel organ.

The cells on its periphery remain prismatic or columnar, but those in its centre become transformed into a stellate network, in which conspicuous nuclei occupy the centre of ramified cells, the processes from which anastomose freely with those of neighbouring cells (see Fig. 66). This conversion of the cells into a stellate reticulum is most marked quite in the centre of the enamel organ; near to its surfaces the processes of the cells are short and inconspicuous, and the whole process strikingly recalls the phenomena of colloid degeneration as observed in certain tumours.

The transformation of the cells occupying the centre and constituting the bulk of the enamel organ into a stellate reticulum goes on progressing from the centre outwards, but it stops short of reaching the layer of columnar cells which constitute the surface of the enamel organ, next to the dentine papilla; a narrow layer of unaltered cells which remain between the stellate cells and the columnar enamel cells constituting the "stratum intermedium."

Thus far all the cells constituting the periphery of the enamel organ are alike: they are columnar or prismatic, but from the time of the appearance of the dentine papilla those which come into relation with it become much more elongated and greatly enlarged, while those round the outer or convex surface of the enamel organ do not enlarge; indeed, according to some authors, they even commence to atrophy at this early period. The cells which lie like

a cap over the dentine germ or "papilla" as they elongate and their nuclei recede to their extremities, take on the character to be presently described as belonging to the "enamel cells," (enamel epithelium, internal epithelium of the enamel organ).

The enamel organ, then, consists (proceeding from without inwards) of an "external epithelium," a "stellate reticulum," a "stratum intermedium," and an "internal epithelium," the external and internal epithelia being continuous at the edges or base of the enamel organ, while at its summit the external epithelium remains still, through the medium of the "neck of the enamel organ," in continuity with the cells of the "stratum Malpighi."

Thus the enamel organ is entirely derived from the oral epithelium, with which, by means of its "neck," it long retains a connection, so that it, and whatever products it may afterwards give rise to, are obviously to be regarded as "epithelial structures." But it is the enamel organ alone which is directly derived from the epithelium; the origin of the dentine germ is quite distinct.

In the embryonic tissue of the jaws, some little distance beneath the surface, and at a point corresponding to that ingrowth of cells and subsequent enlargement of the same which goes to form the enamel organ, appears the first trace of a dentine germ.(1) This appears as a mere increase in the opacity of the part, without at first any visible structural change, and it occupies the concavity of the enamel organ. Thus the dentine germ appears early, indeed almost simultaneously with the formation of a definite enamel organ, but the enamel organ is far in advance of it in point of structural

(1) The term "dental papilla," although eminently convenient, is associated with an erroneous feature of the older views upon tooth development; where it is employed in the following pages, the student must guard against the misconception that free papillæ at any time exist in any animal.

differentiation, and the earliest changes which result in the formation of the enamel organ are strikingly visible before a dentine germ can be discovered. Hence it has been suggested that the enamel organ governs and determines the ultimate form of the tooth. According to Dursy the dark halo which becomes the dentine bulb is, like the inflection of epithelium which forms the enamel germ, continuous all round the jaw, while eventually it develops into prominences at the points corresponding to the enamel germs of future teeth, and atrophies in their interspaces.

From the base of the dentine bulb prolongations pass outward and slightly upwards, so that they in a measure embrace the free edge of the enamel organ, and at a somewhat later period they grow upwards till they fairly embrace the whole enamel organ.

These prolongations of the base of the dentine bulb are the rudiments of the dental sac. In their origin, therefore, the dental sac and the dentine organ are identical, and spring from the submucous tissue: they contrast with the enamel organ, which, as before said, is derived from the oral epithelium.

To recapitulate briefly the facts which are now established beyond all question, the early mammalian tooth germ consists of three parts, one of which, the enamel organ, is derived from the epithelium of the surface; the other two, the dentine organ and the dental sac, originate in the midst of solid embryonic tissue at a distance from the surface, the one is ecderonic or epiblastic, and the other enderonic.

The enamel organ is formed by a rapid increase of cells at the bottom of a process which dips in from the stratum Malpighi of the oral epithelium; the dentine germ and the dental sac are formed in close continuity to this enamel organ from the submucous tissue.

If there were a "basement membrane" demonstrable in the mucous tissues at this early period (which there is

not) the enamel organ and the dentine organ would lie upon the opposite sides of it.

The description of the appearance of the several parts of the tooth germ has brought us to the period at which calcification first commences, but before proceeding further, it will be well to examine more minutely the structure of the several organs in which calcification takes place.

ENAMEL ORGAN.

The enamel organ, as has already been stated, forms a cap-like investment to the dentine bulb, and it is itself thickest over the apex of the latter, thinning down somewhat as it approaches the base.

It is entirely surrounded by an epithelial layer, which upon the inner surface applied to the dentine bulb consists of much elongated columnar cells, and takes the name of *internal epithelium of the enamel organ*, and upon its outer surface the name of *external epithelium of the enamel organ.* The greater bulk of the enamel organ consists of a stellate tissue, which passes gradually through the medium of a layer of rounded cells, the *stratum intermedium*, into the *enamel cells*, or *internal epithelium.* The essential portion of the enamel organ is this layer of "enamel cells," which by their calcification give rise to the enamel, and in lower animals, such as most if not all reptiles, the whole enamel organ is represented by little else than this layer of "enamel cells."

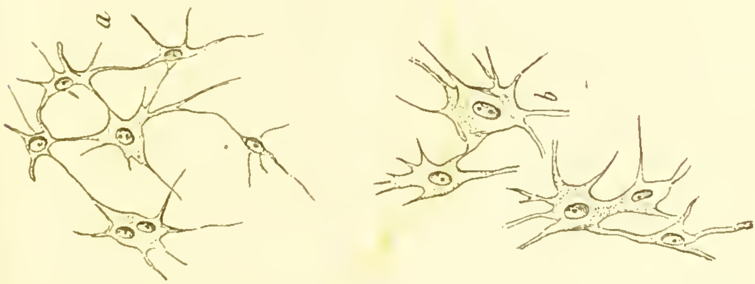
The cells of the internal epithelium (enamel cells) form an exceedingly regular and perfect columnar epithelium, the individual cells becoming by result of their mutual apposition very symmetrical hexagons.

They are four or five times as long as they are broad, and

the nucleus, which is large and oval, occupies that end which is farthest from the dentine. It is said by Waldeyer that the sides of the cells only are invested by membrane, the protoplasm being without investment at its two ends.

Towards the base of the dentine germ, where the internal epithelium merges into the external epithelium, the cells are not so much elongated, and they then pass gradually into the cubical form of these latter cells. At their attached extremities the enamel cells are prolonged into processes

FIG. 66 (1).



which are continuous with the cells of the stratum intermedium, so that it may fairly be concluded that the enamel cells, as they are used up in the formation of enamel, are recruited from the cells of this layer.

The "stratum intermedium" consists of cells intermediate in character between those of the bordering epithelium and the stellate reticulum; they are branched, but less conspicuously so than the stellate cells, with which on the one hand they are continuous, on the other with the enamel cells.

The stellate cells proper are characterised by the great length of their communicating processes, and the interspace of the meshes is occupied by a fluid rich in albumen, so that the consistence of the whole is little more than that of jelly;

(1) Cells of the stellate reticulum of the enamel organ. From Frey's Histology.

as the structure in question constitutes the major part in bulk of mammalian enamel organs, these have been called the enamel jellies, or enamel pulps.

The function and destination of this portion of the enamel organ is not very clear: enamel can be very well formed without it, as is seen amongst reptiles and fish, and even in mammalia it disappears prior to the completion of the enamel, so that the external and internal epithelia come into contact. It has been supposed to have no more important function than to fill up the space subsequently taken up by the growing tooth. (See p. 166).

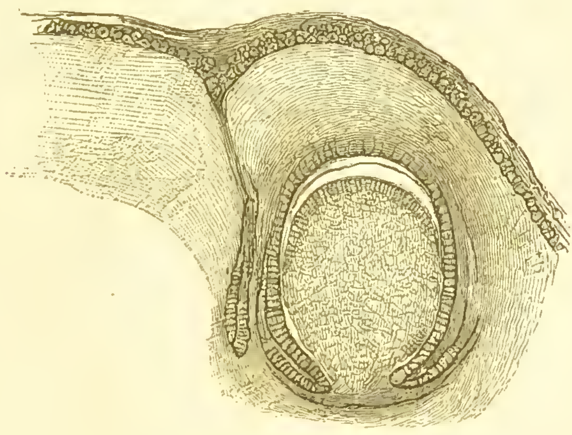
The external epithelium of the enamel organ is composed of cells cubical or rounded in form, and is of little interest save in that it is a matter of controversy what becomes of it. Waldeyer holds to his opinion that, after the disappearance of the enamel pulp and the stratum intermedium, it becomes applied to the enamel cells, and on the completion of the enamel becomes cornified and converted into Nasmyth's membrane. Kölliker and Legros and Magitot dissent from this opinion, the latter stating that the atrophy of these cells commences early, and that they actually disappear prior to the complete atrophy of the organ. For reasons which I have given elsewhere, I do not agree with Waldeyer in this matter, but rather with Magitot. The external epithelium was seen by Nasmyth, Huxley, and Guillot, but it was not very fully described until investigated by Robin and Magitot.

So simple a matter as the vascularity or non-vascularity of the enamel organ is not yet settled; Wedl asserts that it contains no vessels, Magitot and Legros sharing this opinion; Xavier Sudduth has failed uniformly to detect vessels in it, but Dr. Lionel Beale, on the other hand, states that a vascular network lies in the stratum intermedium, and this is confirmed by Professor Howes and Mr. Poulton in the rat.

The inner surface of the enamel organ, where it is applied

to the dentine bulb, presents a perfectly smooth outline, but its outer surface is indented by numerous papillary projections, into which enter blood vessels of the dental sacculus. These papillæ are homologous with, and continuous with those of the gum; they may sometimes be traced along the neck of the enamel germ, and it is believed that they exercise an important influence on the formation of the

Fig. 67 ([1]).



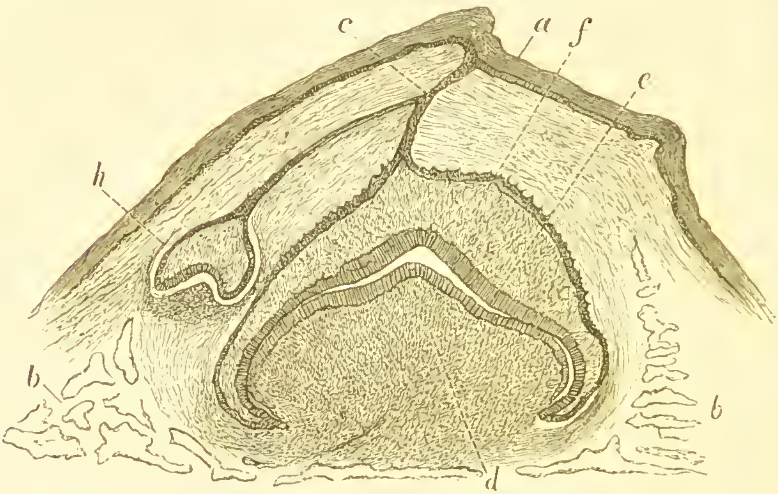
enamel, to which I shall again recur; but their existence is denied by Dr. Sudduth during the active period of the organ.

The narrow attenuated line of cells by which the enamel organ retains its connection with the stratum Malpighi, whence it was derived, varies much in length and direction in different animals; in man it is short and straight; in the calf it is larger, and undulates in its course. It does not remain quite that simple line of cells of which it consisted when first formed, but varicosities, made up of polyhedral cells, bud out from it.

([1]) Dental germ of temporary tooth of an Armadillo, showing its enamel organ, and the enamel germ of the successional permanent tooth to the left of it.

Malassez insists much upon the significance of remnants of epithelium left after the atrophy of the enamel organ; some of these he believes that he has found in the alveolo-dental membrane. This is confirmed, as to develop-

Fig. 68 (1).



ing teeth, by Von Brunn, Archiv f. Mik. Anat., Bd. xxix., who states that in rodents the enamel organ extends far down, in fact, the whole length of the roots, and figures the fibres of the alveolo-dental periosteum as growing through it to take hold of the cementum; but it seems possible that these cells are the same which are by Dr. Xavier Sudduth held to be portions of a lymphatic system.

The origin of the dental germs of the permanent teeth remains to be described: the twenty teeth which have deciduous predecessors being derived from parts of the

(1) From the upper jaw of a kitten about the time of birth. *a.* Oral epithelium. *b.* Bone of jaw. *c.* Neck of enamel organ. *d.* Dentine papilla. *e.* Enamel cells. *f.* Stellate reticulum. *h.* Tooth germ of the permanent tooth, the enamel organ of which is derived from the neck of that of its predecessor.

germs of these, the twelve true molars having a distinct origin. About the sixteenth week of intra-uterine life, from the neck of cells which connects the enamel organ of the temporary enamel germ with the stratum Malpighi, there buds out a secondary inflection of epithelium, similar in appearance to the first rudiment of the enamel germ of the milk tooth; it passes down to the inner side of the temporary tooth sac, and by undergoing a series of changes in all respects analogous with those resulting in the formation of the temporary tooth germ, gives rise to the permanent tooth germ.

The preceding figure (Fig. 68) represents the enamel germ for a permanent tooth budding off from the neck of the enamel organ of the temporary tooth. Many differences of detail, such as the point at which they arise, the depth to which they penetrate into the surrounding parts, and other such characteristics, exist not only between the germs of teeth of different animals, but even between those of teeth situated in different parts of the mouth of the same animal, so that but little importance is to be attached to them.

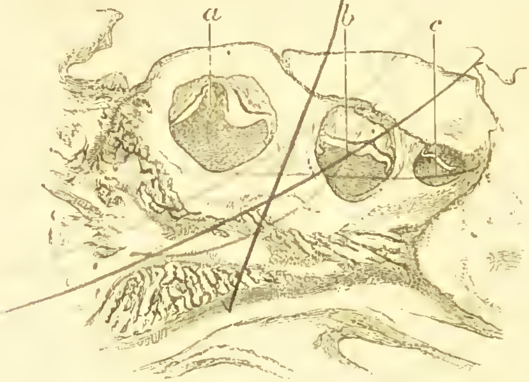
I am indebted to Mr. J. Andrew for a photograph of this section taken from the upper jaw of a fœtus four or five months old, which shows the origin of the germs of the six-year molar well.

At the left-hand side of the figure is seen the germ of the first temporary molar, next that of the second temporary molar, whilst from this is given off the enamel organ of the six-year permanent molar.

Thus the second temporary molar germ gives off two offsets, the one directed to its inner side, which goes to form the germ for the second bicuspid, and one directed backwards for the six-year old molar. From this again will be given off the germ for the second molar, and from that the germ for the wisdom tooth.

The germ of the second permanent molar is believed to originate about the third month after birth, whilst the

Fig. 69 ([1]).



enamel germ of the wisdom tooth succeeds after a much longer interval, *i.e.*, about the third year (Magitot).

Dentine Organ.

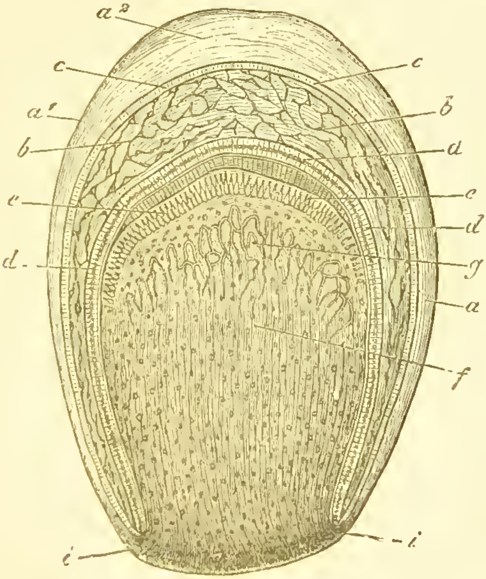
The dentine germ, or dentine bulb, of which the origin has been already described, at first was nothing more than a part of the myxomatous tissue of the jaw which had become more rich in vessels and cells than other neighbouring parts, but did not present any structures essentially different from those found around it. It very speedily assumes the form of the apex of the future tooth, becoming, if it be a canine, simply conical, if a tooth with two cusps, bicuspid ; and coincidently with these changes the layer of cells forming its surface, which is in close relation with the enamel cells, becomes differentiated from the parts beneath it.

These cells, which become dentine by their calcification, form a very distinct layer, which, after the commencement

([1]) From upper jaw of human fœtus. Longitudinal section. Mr. Andrew's specimen. *a.* Germ of first temporary molar. *b.* Germ of second temporary molar. *c.* Cord and germ for 6-year permanent molar. This figure has been lettered upside down.

of calcification, adheres more strongly to the formed cap of dentine than to the rest of the pulp, and so is often pulled away with the former when the two are separated; hence this layer of cells has obtained the name of "membrana eboris," or membrane of the ivory; but the student must beware of falling into the mistake of supposing that it really is a "membrane" properly so called.

FIG. 70 (1).



Before entering upon a detailed description of the transformation which the various cells undergo in their conversion into enamel, dentine, or cementum, it will not be out of place to say a few words relative to the process of calcification generally.

(1) Tooth sac of a calf. *a.* Tooth sac. *a*1 *a*2. Its outer and middle portions. *b.* Stellate cells of enamel organ. *c.* External epithelium of enamel organ. *d.* Internal epithelium of enamel organ. *e.* Odontoblasts. *f.* Dentine bulb in papilla. *g.* Vessels in dentine bulb. *i.* Points where the sac becomes fused with the base of the dentine papilla.

But before doing so it may perhaps assist the student, who may be perplexed in endeavouring to reconcile the statements of various authors, to give a succinct history of the views from time to time set forth. ([1])

Before the time of Goodsir (1838), the development of the teeth was described by Raschkow somewhat vaguely as proceeding underneath the mucous membrane; he did not, however, trace out in what precise manner the several parts of the tooth germ originated. The papers of Goodsir giving, in the place of somewhat vague and general notions, a very definite and intelligible description of observations, was accepted without question by most anatomists, if not by all. Accordingly we find in all the text-books at and after that period, and in some even at the present day, the description given by Goodsir reproduced almost without alteration, so that it will be worth while to briefly relate what his views were.

He believed that at an early period in fœtal life there appeared a continuous open groove, running round the whole circumference of the jaws; that from the bottom of this groove there arose isolated and uncovered papillæ, corresponding in number to the milk teeth; that these papillæ became covered in by the deepening of the groove and the meeting of its two edges over their tops, whilst at the same time transverse septa were formed, so that the several papillæ became enclosed in their own separate follicles. With the details of the process as described by him we are not concerned; it will suffice to remember that he distinguished the four stages: a primitive dental groove, a papillary stage, a follicular stage, and an eruptive stage (the latter of course at a long subsequent period).

Not only were these views accepted quite without question, but they were even extended to explain the development of the teeth in Reptiles and Fishes, and thus in the Odontographies of Professor Owen and Professor Giebel may be found accounts of the development of the teeth in reptiles and fish which are perfectly in accord with Goodsir's theory, but which in fact are far more inaccurate than the same theories were as applied to mammalian teeth.

Even so careful a writer as Professor Huxley, who was the first to point out that these stages really did not exist either in the frog, the mackerel, or certain other fish, accepted them without question as true of mammalia. Marcusen ([2]) (1849) gave upon the whole a

([1]) After the present summary had been partly prepared, the author met with the very excellent *résumé* given by Messrs. Legros and Magitot, from which he has received much assistance.

([2]) In the *résumé* given by Messrs. Legros and Magitot, before referred to, due credit is not given to the papers of Marcusen and Huxley (1849, 1854) (although they are alluded to), and it appears to me that too much is given to that of Natalis Guillot (1858).

correct account of the process, referring the enamel to the oral epithelium, and Professor Huxley (1854), whilst demonstrating that the stage of free papillæ was not to be found in certain fish and reptiles (a fact also made out in the newt by Dr. Beale), clearly and strongly expressed the same view as to the origin of the enamel organ, and hence of the enamel. And whilst regretting that their hold upon the minds of anatomists has been so strong as to encourage deductions therefrom going wider and wider of the mark, I would not be understood to set small value upon the observations of Arnold and Goodsir. They were a great step in advance, and were as accurate as the methods of investigation then in use would allow of : moreover, the error in observation is very easy to account for, as, the epithelium having peeled off as a result of decomposition, or the use of weak spirit, the state of things left does not widely differ from that described by Goodsir.

The subject rested for many years without further advances, but in 1863 Professor Kölliker demonstrated, beyond all cavil, the real origin of the enamel organ and its relations to the oral epithelium, the dentine organ, and the dental sac.

His views, substantially correct, have been elaborated by Waldeyer, Kollmann, Hertz, Legros and Magitot, Wedl, and others, but only in minor particulars have they been modified.

The development of the teeth of reptiles was found by a pupil of M. Kölliker's, M. Santi Sirena, to have several features in accord with that of mammalian teeth; my own researches on the teeth of Batrachia and Fish and Reptiles, elsewhere detailed, have proved a striking general similarity in the process throughout the vertebrate kingdom.

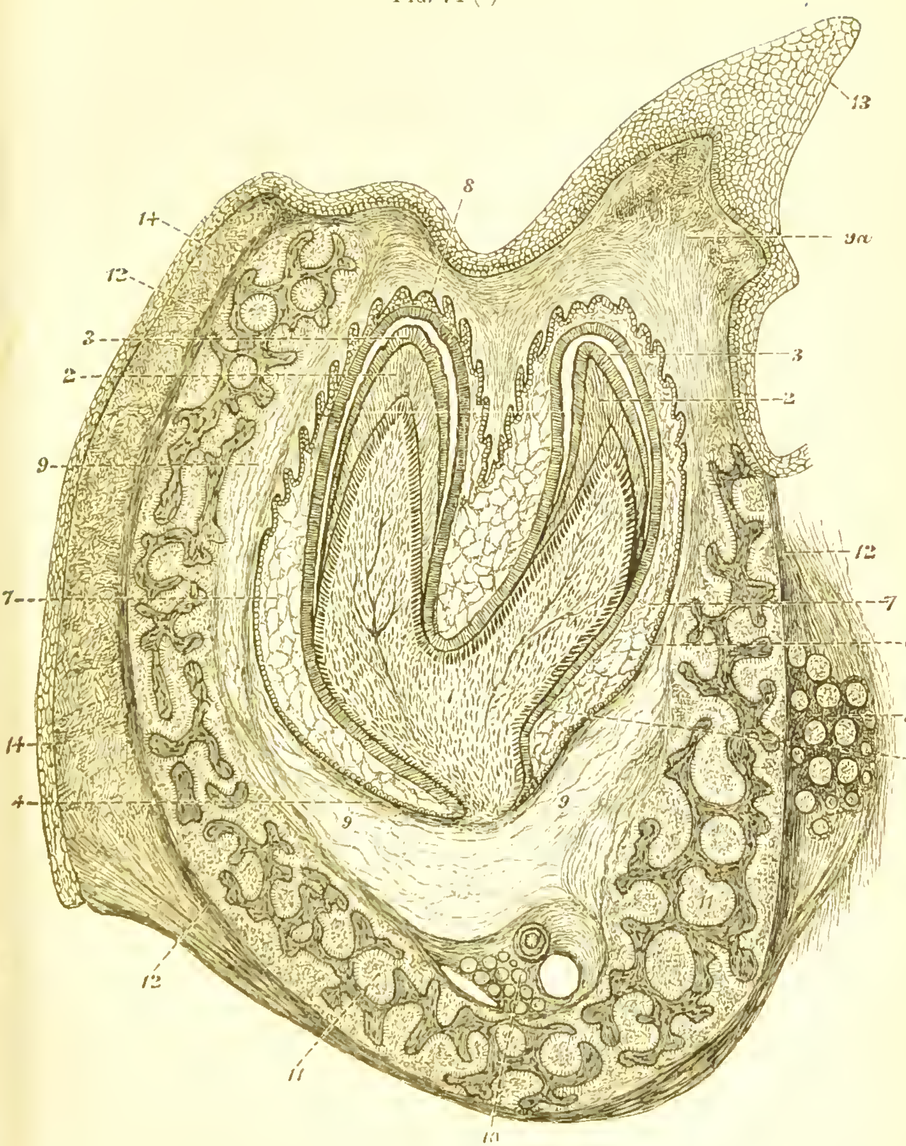
Dental Follicle.—In the foregoing account little mention has been made of the tooth follicle or tissue forming a capsule-like investment around the dentine germ and enamel organ. At an early period of development the tissue forming the dentine papilla of a mammalian tooth is seen to be prolonged outwards and upwards from its base (see *h* in Fig. 65); these processes appear to grow rapidly upwards, so as to embrace the enamel organ; but whether this is really so, or whether it is merely that the ill-defined tissue in which the dentine forming organ has itself originated is in this region also becoming more pronounced, it is hard to say; probably the latter is the more true. This up-growth from the base of the dentine papilla is the first appearance of a special dental sacculus, which is thus derived from

sources identical with that of the formative organ of the dentine.

While these changes are going on, the tooth sac is becoming lodged in a widely open gutter of bone, which is being rapidly formed at its sides and under its base. If at this stage (see Fig. 71) the gum be stripped off the jaws, the developing tooth capsules are torn off with it, and are inseparable from it except by actual cutting, thus leaving the gutter of bone quite bare and empty. In fact the capsule or sac which encloses the tooth germ consists of almost the whole of the connective tissue which intervenes between the special dentine and enamel germs and the bone, which latter is originating deep in the tissues and independently of the periosteum, which is not yet differentiated.

In the first instance the follicle wall is only distinguished from the connective tissue external to it by being somewhat richer in cells, vessels, and fibrillar elements; being, in fact, more condensed or more compact. The sacs, when at their fullest development, are divisible into two layers, an outer thin firm wall, and an inner looser tissue, not very dense. At the base of the tooth sac, the follicle wall is not separable nor distinguishable from the base of the dentine papilla with which it blends. The follicle wall is richly vascular; and over the surface of the enamel organ it is prolonged inwards in the form of villous or papilliform eminences (8 in Fig. 71), projecting into the external epithelium of the enamel organ; to these prominences, which are analogous to the papillæ on the free surface of the gum, some authors attach much importance, as having an influence upon the direction of the enamel prisms, and so regulating the pattern formed; but this view is by no means universally accepted. The internal or softer and looser portion of the follicle wall, which has a consistency but little firmer than that of the stellate reticulum of the enamel organ, is much developed in Ruminants, where there is to be a deposition

Fig. 71 (1)



(1) Transverse Section of the Lower Jaw and Developing Back Tooth of a Lamb, copied from Waldeyer (Henle's Zeitschrift f. Rat. Med. 1865). In its outlines the figure is faithful to nature; it is so far diagrammatic that more of structure than could be seen with the magnifying power employed is introduced.

1. Dentine germ, with its border of odontoblasts. 2. Formed dentine. 3. Formed enamel. 4. Points where the inner epithelium and the outer epithelium of the enamel become continuous. 5. Enamel cells or internal epithelium. 6. External epithelium of enamel organ. 7. Stellate reticulum of enamel organ. 8. Papillary projections into the enamel organ. 9. Connective tissue around the sac, becoming continuous above with that of the gum (9a); this constitutes what is called the tooth sac. 10. Vessels and nerves of the jaw. 11. Bone of lower jaw. 12. Periosteum of the jaw. 13. Heap of epithelium over the young tooth. 14. External skin with its epidermis. 15. Muscular bundles from floor of mouth.

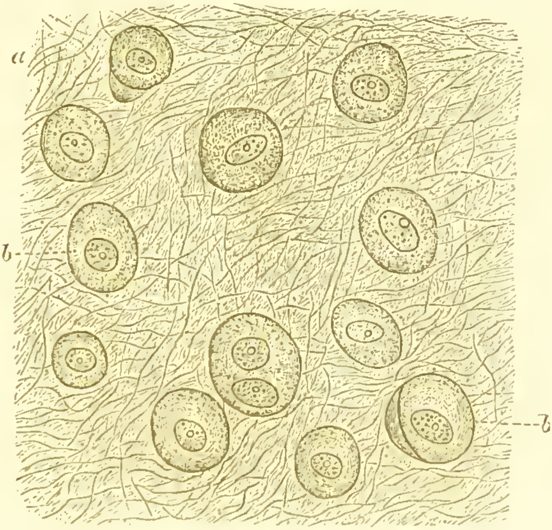
[*To face p.* 152.

of coronal cement. This differentiation of a portion of the dental sac is thought by Messrs. Legros, Robin, and Magitot to be sufficiently pronounced to justify its designation as a distinct "cement organ."

The Cement Organ.

Cementum is, according to these authors, developed, just as bone is, in two distinct methods.

Fig. 72 [1].



Where it is not to be very thick, and is to clothe roots, the ossification takes place in membrane (the alveolo-dental periosteum), but where it is to form a thick layer over the crown, as in Ruminants, a cartilaginous cement organ is formed, and we have a calcification analogous to formation of bone in cartilage.

Thus the cement organ is found in those animals only

[1] Cement organ of a calf (after Magitot). *a.* Fibroid matrix. *b.* Cartilage cells and capsules.

From Magitot. Comptes Rendus, 1874.

Stage of the Embryo.			Temporary Dentition.					Permanent Dentition.					
Its length from the vertex to the heel.	Total weight.	Corresponding age.	Central Incisor.	Lateral Incisor.	1st Molar.	2nd Molar.	Canine.	Central Incisor.	Lateral Incisor.	Canine.	1st Pre-molar.	2nd Pre-molar.	1st Molar.
Inches.	Grains.												
1·18	46·2 to 53·9	7th week.	At this date one observes at the edge of the jaw of the embryo only the epithelial eminence and the epithelial inflection of Kölliker. The superior maxillary and intermaxillary bones are not united, and the inferior maxillary arch contains Meckel's cartilage only, without any trace of bone. It is in the course of this 7th week that the epithelial bands (enamel organs) of the temporary teeth are successively formed in the order of their designation.					No trace of the follicles.					
1·18 to 1·57	154 to 184·8	9th week.	At this date appears in juxtaposition with the downward extremity of the epithelial band the first trace of the dentine bulb. This stage occurs nearly simultaneously for the whole series of the temporary follicles.					No trace of the follicles.					
1·57 to 2·36	693 to 739·2	10th week.	At this period the wall of the follicle detaches itself from the base of the bulb and rises up its sides. This stage occurs in the same order as the preceding.					No trace of the follicles.					
5·90 to 7·08	1540 to 1848	15th week.	The wall of the follicle continues its development. The epithelial germ commences its transformation into an enamel organ.										Appearance of the enamel germ springing from the epithelial inflection.
7·08 to 7·48	1848 to 2772	16th week.	The wall of the follicle is closed. The epithelial band is broken and the follicle is thenceforward without any connection with the epithelium of the surface.					Appearance of the epithelial band derived from the neck of the enamel organ of the corresponding deciduous tooth.					

			Central Incisor.	Lateral Incisor	1st Molar.	2nd Molar.	Canine.		
7·87 to 8·26	2772 to 3388	17th week	Appearance of the cap of dentine.				Appearance of the cap of dentine.		Appearance of the bulb.
8·26 to 9·44	3394 to 3858	18th week 4 months.			Appearance of the dentine cap.				Appearance of the wall of the follicle.
9·84 to 10·63	4322 to 6945	20th week.	Dimensions in vertical height of the cap of dentine. ·059	·059	·039	·039	·059	Appearance of the dentine organ.	Enclosure of the wall and rupture of the band.
12·59 to 13·77	15434 to 23152	25th week 6 months.	·07	·07	·054	·054	·07	The wall of the follicle which appeared after the 21st week has already acquired a certain distinctness.	Appearance of the cap of dentine.
14·56 to 15·35	23152 to 30868	28th week 6½ months.	·093	·093	·078	·078	·093	The wall of the follicle continues its development; the epithelial germ commences its transformation into an enamel organ.	The cap of dentine is from ·003 to ·007 inches in height.
15·74 to 16·53	30868 to 38585	32nd week 7½ months.	·113	·113	·093	·093	·113	Continuation of the same developmental processes.	The cusps of dentine which originate upon the several apices of the dentine organ have coalesced.
17·32 to 18·50	38585 to 46302	36th week 8½ months.	0·118	0·118	0·109	0·109	0·118	Continuation of the same developmental processes.	The cap of dentine is from ·004 to ·039 inches in height.
17·71 to 20·47	46302 to 54019	39th week 9 months.	0·136	0·136	0·118	0·118	0·136	Closure of the wall of the follicle. The cap of dentine has not appeared; its formation only takes place in the 1st month after birth.	The cap of dentine is from ·039 to ·078 inches in height.

which have coronal cement, such as the Herbivora. In a calf embryo about the time that dentine calcification is commenced, there may be distinguished beneath the follicle wall and above the enamel organ a greyish layer of tissue, thick enough to be distinguishable with the naked eye, and of firmer consistence than the enamel organ, from which it also differs in being richly vascular.

But though it exists at this early period, it is not till later, when, after the completion of the dentine and enamel immediately beneath it, its own function is about to come into play, that it attains to its characteristic structure. This M. Magitot designates as fibro-cartilaginous, as there appear in it characteristic cartilage cells or chondroplasts, containing one, two, or rarely three cells, which have spherical or ovoid nuclei.

In those creatures which have cementum upon the roots of the teeth only, no special cement organ exists, but osteoblasts which calcify into cementum are furnished by the tooth sac.

It is said that the inner layer of the tooth sac is concerned in the formation of the cement; that the outer layer, conjointly with the surrounding connective tissue, is converted into the alveolo-dental periosteum, but I cannot myself recognise the justice of this distinction in practice. In human teeth the parts of the follicle wall or sac cease to be distinctly distinguishable at a comparatively early period, and their importance is not such as to call for very detailed description.

Another structure, once thought important, and now known to be a mere bundle of dense fibrous tissue, is the "*gubernaculum*." The permanent tooth sacs, during their growth, have become invested by a bony shell, which is complete, save at a point near their apices, where there is a foramen. Through this foramen passes a thin fibrous cord, very conspicuous when the surrounding bone is broken

away, which is called the "*gubernaculum*," from the notions entertained by the older anatomists that it was concerned in directing or effecting the eruption of the tooth. The gubernacula of the front permanent tooth sacs perforate the alveolus and blend with the gum behind the necks of the corresponding milk teeth; those of the bicuspids uniting with the periosteum of the alveoli of their deciduous predecessors.

Calcification.

A tissue is said to be "calcified" when the organic structures of which it is composed are hardened and stiffened by impregnation with salts of lime. The impregnation with lime salt may go on so far that the residual organic matrix is reduced to a very small proportion, as is exemplified in the case of adult enamel, in which the organic constituents make up only from one to three per cent. of the whole, so that practically the enamel wholly disappears under the influence of an acid; or the organic matrix may persist in sufficient quantity to retain its structural characteristics after the removal by solution in an acid of its salts, as is the case with dentine, bone, and cementum. There are two ways in which a calcified structure may be built up: the one by the deposition of the salts in the very substance of a formative organ, which thus become actually converted into the calcified structure; the other by a formative organ shedding out from its surface both the organic and inorganic constituents, and thus, so to speak, excreting the resultant tissue.

An example of the latter method is to be found in the shells of many mollusks, in which the mantle secretes the shell, and is able to repair fractures in it, without itself undergoing any apparent alteration; while the formation of

dentine, bone, and enamel ([1]) are examples of calcification by conversion.

The insoluble salts of lime are altered in their behaviour by association with organic compounds, a fact which was first pointed out by Rainie, and has been more recently worked out by Professor Harting and Dr. Ord.

If a solution of a soluble salt of lime be slowly mixed with another solution capable of precipitating the lime, the resultant lime salt will go down as an amorphous powder, or, under some circumstances, in minute crystals. But in the presence of gelatine, albumen, and many other organic compounds, the form and physical character of the lime salts are materially altered, and in the place of an amorphous powder there are found various curious but definite forms, quite unlike the character of crystals produced without the intervention of the organic substance.

Mr. Rainie found that if calcium carbonate be slowly formed in a thick solution of mucilage or albumen the resultant salt is in the form of globules, laminated in structure, so that the globules may be likened to tiny onions; these globules, when in contact, becoming agglomerated into a single laminated mass, it appearing as if the laminæ in immediate apposition blended with one another. Globular masses, at one time of mulberry-like form, lose the individuality of their constituent smaller globules, and become smoothed down into a single mass; and Mr. Rainie suggests as an explanation of the laminated structure that the smaller masses have accumulated in concentric layers which have subsequently coalesced; and in the substitution of the globular for the amorphous or crystalline form in the salt of lime when in contact with various organic substances, Mr. Rainie claimed to find the clue for the explanation of the development of shells, teeth, and bone. At this point

([1]) All observers are not, however, agreed as to the formation of the enamel nor of dentine.

Professor Harting took up the investigation, and found that other salts of lime would behave in a similar manner, and that by modifying the condition of the experiment very various forms [1] might be produced. But the most important addition to our knowledge made by Professor Harting lay in the very peculiar constitution of the "calcospherites," by which name he designated the globular forms seen and described by Rainie. That these are built up of concentric laminæ like an onion has already been mentioned, and Mr. Rainie was aware that albumen actually entered into the composition of the globule, since it retained its form even after the application of acid.

But Professor Harting has shown that the albumen left behind after the treatment of a calcospherite with acid is no longer ordinary albumen; it is profoundly modified, and has become exceedingly resistant to the action of acids, alkalies, and boiling water, and in fact resembles chitine, the substance of which the hard skins of insects consist rather than any other body.

For this modified albumen he proposes the name of "calcoglobulin," as it appears that the lime is held in some sort of chemical combination, for the last traces of lime are retained very obstinately when calcoglobulin is submitted to the action of acids.

The "calcospherite," then, has a true matrix of calcoglobulin, which is capable of retaining its form and structure after the removal of the great bulk of the lime.

Now it is a very suggestive fact that in the investigation of calcification we constantly meet with structures remarkable for their indestructibility: for example, if we destroy the dentine by the action of very strong acids, or by variously contrived processes of decalcification, putrefaction, &c., there remains behind a tangled mass of tubes, the

(1) Thus he was successful in artificially producing "dumb-bell" crystals.

"dentinal sheaths" of Neumann, which are really the immediate walls of the dentinal tubes.

Or if bone be disintegrated by certain methods there remain behind large tubes, found to be the linings of the Haversian canals (Kölliker), and small rounded bodies, recognisable as isolated lacunæ; and in the cuticula dentis we have another excellent example of this peculiarly indestructible tissue.

In point of fact, as will be better seen after the development of the dental tissue has been more fully described, on the borderland of calcification, between the completed fully calcified tissue and the formative matrix as yet unimpregnated with lime, there very constantly exists a stratum of tissue which in its physical and chemical properties very much resembles "calcoglobulin."

It should also be noted that globular, spherical forms are very constantly to be seen at the edges of the thin cap of forming dentine, and may be also traced in and around the interglobular spaces (see Fig. 35); moreover, isolated spherules of lime salt have been described by Messrs. Robin and Magitot as occurring abundantly in the young pulps of human teeth, as well as those in the herbivora, where their presence was noted by Henle; perhaps all deposit of lime salts commences in this way.

Calcification of the Enamel.

Although the calcification of the dentine commences before that of the enamel, it will be convenient to describe that of the enamel first, as being a somewhat simpler and more easily intelligible process.

As has already been mentioned, I am distinctly of opinion that the enamel is formed by the actual conversion of the cells of the enamel organ into enamel, but as this view is

not held by all who have written upon the subject, I will first mention the alternative theory, namely, that the enamel is in some sense secreted or shed out by these cells. In support of this latter theory the names of no less authorities than Professor Huxley, Kölliker, Wenzel, and Magitot, may be adduced, but the grounds on which their decisions are based are appearances susceptible of a different interpretation. Kölliker considers that the cells do not undergo any direct conversion, but that the enamel is shed out from the ends of the enamel cells, the enamel fibres therefore corresponding in size and being continuous with the enamel cells whence they were shed out.

The cells would thus elaborate, and so to speak, plaster on from their free ends the material in question upon the already formed enamel, they themselves retaining their own integrity. In support of this view may be cited the close resemblance in the resultant products in the case of enamel, and of the shells of certain mollusks, say, for example, Pinna. In the case of the mollusk the shell is formed intermittently by the margins of the mantle, which are closely applied to it, but are at any time separable, so that it is difficult to suppose that any conversion of its constituent cells can take place; but it would rather seem certain that something must be shed out from their ends, which is hardened by the deposition in or with it of lime salts. The shell of Pinna contains so large an amount of organic matter that its structure is retained even after the removal of the lime by means of an acid, and it is conceived that the cells of the mantle are at work, like so many bees plastering wax upon a honeycomb, elaborating and plastering on their products so that each one builds on to its own prism and retains for this its individuality.

But whether the enamel cells manufacture something which they shed off from their ends, or are themselves converted into hard tissue by the deposition of lime within their own

substance, no one doubts that they preside over the process, and determine the form of the result.

Professor Huxley's reason for doubting the direct conversion of the enamel cells into enamel was that a membrane could be raised from the surface of growing enamel, at any period of its development, by the use of acid reagents, this membrane necessarily intervening between the formed enamel and the enamel cells; hence he denied that the enamel organ contributed in any way directly, though it might indirectly, to the development of the enamel.

To the nature of this "membrane" I shall have again to refer, so that for the present it will suffice to say that the structure in question cannot be demonstrated, and in fact has probably no existence, prior to the use of the reagent.

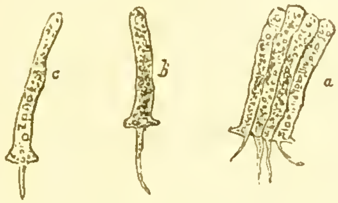
The cells of the internal epithelium of the enamel organ or enamel cells have been already in some measure described: they are elongated cells, forming a very regular columnar epithelium, and are hence rendered hexagonal by mutual apposition; they vary in their length and diameter in different animals.

To secure uniformity of nomenclature, the name ameloblast has recently been proposed for them, as being better comparable with the terms odontoblast and osteoblast.

Although they are connected with the cells of the stratum intermedium by a process at their base, they often adhere more strongly to the enamel, when once this has begun to be formed, than to the rest of the enamel organ, so that when a dental sac is opened the enamel cells are most easily obtained by scraping the surface of the enamel. The cells thus torn away often have tapering processes at the ends directed towards the enamel, which were first described by my father, and go by the name of "Tomes' processes." The cells are also slightly enlarged at these extremities, especially if they have been immersed in glycerine or any such fluid which causes their shrinkage, for this end of the cell having

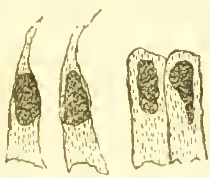
received a partial impregnation with lime salt at its periphery, and so being rigid, is unable to contract with the rest of the cell. These enlarged, everted ends, often show a very

Fig. 73 (1).



sharp contour, their trumpet-like mouths tending to confirm the statement of Waldeyer that the protoplasm of the cell is not covered in by membrane at its ends. The ends of the enamel cells near to the formed enamel are granular, this granularity being due to the deposition there of calcareous

Fig. 74 (2).



particles, as is indicated by its clearing up when treated with dilute acids. The impregnation with calcareous salts commences at the free end of the enamel cell, and at the periphery before the central portion, and it is to this fact that the existence of "Tomes' processes" is due, for when the enamel cell is dragged away from the formed enamel prism, it separates across the line of calcification; and thus the axial part of the cell, when torn away, projects out further

(1) Enamel cells with Tomes' processes.

(2) Enamel cells; the two on the right have been shrunk by immersion in glycerine, and present the open trumpet-shaped ends described in the text.

than its periphery, in consequence of calcification having extended less far at this central portion of the cell.

In other words, if the forming enamel were freed from the adherent enamel cells, its surface would be pitted, each little pit marking the centre of an enamel prism ; and if a thin section of this immediate surface could be taken off, it would be pierced with holes at regular intervals.

The enamel cell with its process is like an odontoblast with a very short dentinal fibril, which has been pulled out of the formed dentine, and the nature of the "Tomes' processes" is well illustrated in the enamel organs of marsupials. It will be remembered that their enamel is permeated by a large number of canals, which become continuous at the junction of the dentine and enamel with the dentinal tubes. Accordingly the enamel cell of a marsupial, engaged in the formation of a permanently tubular enamel, is just like an odontoblast in that it has a long, fine process, pulled out of the already formed enamel.

As the youngest part of the enamel has by no means attained to its full hardness, it is quite possible to obtain, in small pieces, sections parallel to its surface; the nearer they are to the surface, the larger will be the perforations, showing what has already been stated respecting calcification commencing at the periphery of each cell to be true. And it is possible, by the use of an acid, to obtain such sections upon a larger scale, for under the influence of such a reagent, this youngest layer of the enamel sometimes peels off in a sheet, bringing with it in places enamel cells, in places enamel prisms, adhering to its opposite sides. When destitute of adherent enamel cells or prisms, this so-called membrane is foraminated; and the processes of the ends of the enamel cells are fitted into and passed through these perforations.

The real nature of the membrane which could be raised from the surface of growing enamel was first demonstrated

by my father, and his explanation has been accepted by Waldeyer and other authorities; it will be seen that this sheet, produced solely by the destructive action of reagents, corresponds with the membrana preformativa of some writers (see page 181), and with the membrane described by Professor Huxley as intervening between the enamel cells and the enamel. Hence it will be seen that the fact of acids raising a membrane from the surface of the enamel does not really militate against the theory that the enamel is due to the direct conversion of the enamel cells into enamel.

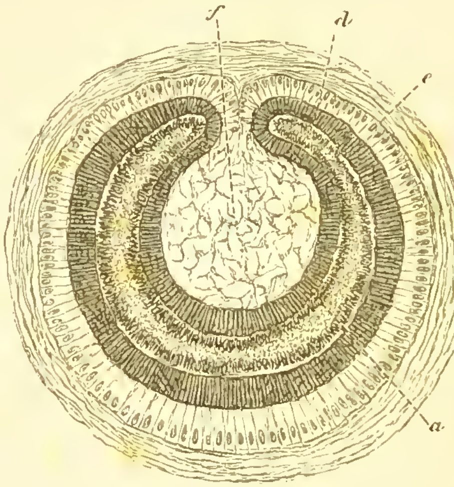
The cells on the one side of the membrane readily separate from one another, adhering, however, slightly by their dilated ends (*vide* supra), and the fact that we are able to isolate the youngest layer of enamel as a thin sheet, is probably to be explained by its chemical nature. It appears to belong to that class of peculiarly resistant substances which are to be found on the borders of calcification, and behaves very much like Professor Harting's "calcoglobulin" (see page 159); at all events it may safely be said to have undergone some chemical change preparatory to the reception of its full amount of lime salts.

The calcification of the enamel should be so complete that its fibrous structure is but slightly apparent in longitudinal sections, and the individual fibres should appear structureless, with the exception of the feebly marked striation (see page 55). In enamel of imperfect structural character the centre of the fibre is not completely calcified, the arrest of development having taken place short of its full conversion.

The stellate tissue of the enamel organ disappears long before the whole thickness of the enamel is formed, and changes go on in the latter up to the time of the eruption of the tooth; the enamel of a tooth prior to its eruption having a chalky, opaque surface.

The enamel of the teeth of reptiles is developed from an enamel organ which at no time possesses a stellate tissue; this is also the case in all fish which I have hitherto ex-

FIG. 75 (1).



amined. In the poison fangs of snakes the enamel cells, over the interior of the poison tube, where no enamel exists, appeared to be transformed into a stellate reticulum, which change in this case would appear to be a retrograde metamorphosis.

The nuclei of the enamel cells, which lie at the extremities furthest from the enamel, appear to recede as calcification goes on; they do not exercise any special influence on the process as far as can be seen.

(1) Transverse section of the tooth sac of a poison fang (Viper). The crescentic pulp (*a*) is surrounded by a layer of dentine (*d*); external to this is a layer of columnar enamel cells, which, upon the exterior of the tooth, upon which a thin layer of enamel is to be formed, are large conspicuous cells. Where they pass in between the horns of the crescent, into that part which will ultimately be the poison canal, their character is lost, and their place taken by stellate cells (*f*). No enamel is formed in this latter position.

As has been already mentioned, Kölliker dissents from the above account of the calcification of the enamel, partly on the ground that enamel cells may be seen of the same size and form at all stages of the formation of enamel.

The process he regards as one of secretion, the enamel being shed out, so to speak, from the free end of each enamel cell; hence the prisms of the enamel will correspond in size and number with the cells of the enamel epithelium; the processes of the enamel cells he regards as being fragments of this hardened secretion which are still clinging to the parent cell.

M. Magitot (Journal de l'Anatomie de M. Ch. Robin, 1879), revived this view, describing each cell as terminated, towards the forming enamel, by a little plate of dense material through which by some process of exosmosis the constituents of enamel travel out. He notes that these plates often cohere so as to form a sheet (cf. page 164), but says nothing of their being perforated. No one, however, who had seen the enamel cell of a marsupial with the tapering process five or six times as long as itself which had been pulled out of the young enamel would be satisfied with the excretion theory.

The reasons for adopting the opposite view will have been gathered from the text: they are, in brief, the occurrence of the "Tomes' processes," especially in marsupials; the rigidity of the open mouths of the enamel cells; the pitted surface of the youngest layer of enamel, the foraminated membrane which can be raised from it, and the relation of these facts to the occurrence of the processes of the enamel cells.

Schwann believed that the enamel cell was constantly increasing at its free end (*i.e.*, that next to the enamel), and that the new growth, or youngest part of the cell, is calcified as fast as it is formed; this view differs little from that of Kölliker, who prefers to express it by saying that this end of the cell is constantly shedding off or secreting a material which becomes external to itself. My father, Waldeyer, Hertz, and many others, believe that the cell growth takes place not at this free end, but at the attached nucleated end, and that it is the oldest portion of the cell itself which receives an impregnation with salts and forms the enamel.

Professor Huxley's opinion (page 161) is, I take it, based on the fact that a membrane could be raised from the surface of young enamel, which must have intervened between the enamel cells and the enamel prisms; if my father's explanation of the nature of this membrane be accepted, the difficulty vanishes.

My own researches upon the development of the teeth of fishes also furnish evidence tending in the same direction; as has been already mentioned, the enamel cells in some parts of the enamel organs of certain fish, such as the eel and perch, and certain Batrachia, *e.g.*, the newt, have dimensions very greatly exceeding those of the cells in the remainder of the organ. These highly developed cells, three times as long as the corresponding cells lower

down upon the dentine papilla, are in the position of the terminal cap of enamel which characterises these teeth. Moreover, in the tooth sac of the poison fang of a viper, the distribution of the large cells coincides with that of the enamel on the finished tooth.

Calcification of the Dentine.—The dentine is formed upon the surface of the dentine bulb, or papilla, from without inwards, so that no portion of dentine once calcified can receive any increase in external dimensions; all additions must take place upon the interior of the dentine cap. The nature of the dentine bulb has already been to some extent described; it remains to consider somewhat more minutely the nature of its surface. The cells constituting the membrana eboris, to which Waldeyer has given the convenient name of "odontoblasts," form an exceedingly sharply defined layer upon the surface of the dentine wall, being arranged in a single row; the cells immediately beneath them differ strongly from them, so that there is not so marked an appearance of transitional structure as may be seen in the stratum intermedium of the enamel organ. Nothing whatever like the linear succession of formative cells, which, by coalescence at their ends went to form the dentinal tubes, as described by the older writers, is to be seen.

The odontoblast cells vary in form according as the dentine formation is actively going on or not, but at the period of their greatest activity they are broad at the end directed towards the dentine cap, so as to look almost abruptly truncated. The several processes of the cells have already been described; there are, however, sometimes several "dentinal processes" proceeding from a single cell, and Boll has counted no less than six.

The cells are finely granular, and are, according to Waldeyer and Boll, destitute of all membrane; the nucleus is oval, lies in that extremity of the cell which is farthest from the dentine, and is sometimes prolonged towards the dentinal process so as to be ovoid or almost pointed.

The dentinal process passes into the tubes of the dentine, and it frequently happens that when the membrana eboris is only slightly separated from the dentine these processes, which constitute the dentinal fibrils, may be seen stretching across the interval in great numbers.

The odontoblasts, as may be seen from Figs. 31 and 77, are fitted closely together, and there is not much room for any other tissue between them, so long as the formation of dentine is actively going on. Prior to its commencement, however, the cells are not so square at their ends, and the appearance of the thin edge of such a pulp suggests the idea that they are bedded in a transparent and structureless jelly, which projects a little beyond them. To render my meaning more clear by a homely illustration, the surface of the pulp at this stage reminds one of the clear jellies put upon the table with

Fig. 76 [1].

strawberries or the like buried in them, near to, but beneath, the surface. But no such substance can be distinctly seen when once calcification has actively set in.

When the pulp has completed, for the time being at all events, the formation of the dentine, the odontoblast cells become more elongated and more rounded in their outline and taper off towards and into the dentinal process, instead of having truncated ends.

The cells figured by Lent as the formative cells of dentine, I regard as odontoblasts taken from an adult tooth, the period of formative activity being past, and I am inclined to

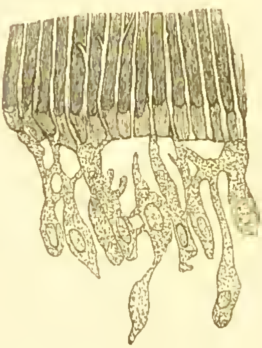
[1] Isolated odontoblast cell.

think that his views on the subject of development are open to criticism, as being based upon the appearances presented by such old cells.

The dentine is, I believe, formed by the direct conversion of the odontoblast cells, just as is the enamel by that of the enamel cells, and is derived from them, and from them alone.

According to this view, which is supported by Waldeyer, Frey, Boll, Dr. Lionel Beale, and many other writers, the dentinal fibrils, the dentinal sheaths, and the matrix between

Fig. 77 [1].



these latter, are alike derived from the metamorphosis of the odontoblast cell. In other words, the three structures in question may be taken as being three stages in the conversion of one and the same substance: thus we have the dentinal fibril in its soft condition, little more than the unaltered protoplasm of the cell; then the dentinal sheath, one of those peculiarly resistant substances which lie on the borders of calcification; and lastly, the matrix, the completed, wholly calcified tissue.

That some such relation exists seems to be indicated by the fact that dentinal tubes once formed are capable of further calcification, by which their calibre becomes sensibly diminished. Thus, my father states (speaking of the incisor

[1] Odontoblasts *in situ*. After Waldeyer.

teeth of rodents), "the tubes which proceed from the pulp cavity near the base of the tooth, are, in most cases, perceptibly larger than those that are situated higher up; hence it follows that, as the latter were once near the base of the tooth, the dentinal tubes undergo a diminution of calibre after their original formation. In the teeth of the Sciuridæ I have found a difference of size amounting to a third or half between the tubes near the base and those near the surface in wear."

And Dr. Lionel Beale calls attention to the fact that the hollows of the canals are largest nearest to the pulp, and smallest at the periphery of the tooth—in other words, at the oldest part; also that calcification is still slowly going on even in advanced life, so as often to lead to the obliteration of the peripheral tubes. There is, too, the statement of Robin and Magitot, that the teeth become more rich in calcareous salts as age advances, so that analyses of human teeth show great discrepancies.

It is difficult to see how a dentinal tube once formed can become contracted to a third or half of its diameter unless we believe that that which was at first the soft tissue (dentinal fibril) occupying its canal may become at its periphery metamorphosed into "dentinal sheath," while that which was originally this latter has passed into the condition of matrix.

But it is quite probable that the dentinal sheath has no separate existence in the dentine until after its disintegration by a strong acid.

As I have elsewhere expressed it, the most external portions of the odontoblasts undergo a metamorphosis into a gelatigenous matrix, which is the seat of calcification, while their most central portions remain soft and unaltered as the fibrils. Intermediate between the central permanently soft fibril and the general calcified matrix, is that portion which immediately surrounds the fibril, namely, the

dentinal sheath; as expressed by Dr. Lionel Beale they are protoplasm, formed material, and calcified formed material.

Just as in the case of enamel, there are writers who hold that the odontoblasts are not themselves converted into dentine, but that they preside over the secretion of a material which is. Thus Kölliker and Lent believe that while the canals and their contents are continuations of the odontoblasts, the matrix is a secretion either from these cells or from the rest of the pulp, and so is an "intercellular" substance. Their view is therefore intermediate between the excretion and conversion theories; and Kölliker goes on to say, "since the dentinal cells are immediately drawn out at their outer ends into the dentinal fibres, and do not, as was formerly thought, grow out in such a manner that the dentinal fibre is to be regarded only as the inner part of the cell, so it is not possible to derive the dentine immediately from the cells." But is not Professor Kölliker thinking and writing of those aged, spent cells which his pupil Lent figured? No one could speak of a young, active odontoblast as "drawn out into the dentinal fibril." A good section of young developing dentine shows that the cells are square and abrupt towards the dentine; they do not taper into the dentinal process in the smallest degree, and there is no room for any intercellular substance whatever.

Hertz coincides with Kölliker in regarding the matrix as a "secretion from all the dentinal cells in common which stands in no definite histological relation to the individual cells," but his figure also I believe to be representative of an adult inactive surface of pulp, in which dentine formation has almost ceased.

Kölliker and Lent are of opinion that a single cell is sufficient to form the whole length of a dentinal fibril, not having seen evidence of active cell growth in the subjacent layer of the pulp, from which they would infer that the membrana eboris was supplemented by new cells from below. In a later edition, however, Kölliker speaks with much more hesitation on this point.

Magitot (1881) holds that the whole of the dentine is "a product elaborated by the odontoblasts," but neither selected by nor formed by the conversion of the odontoblasts, and he denies the existence of the sheaths of Neumann *in toto*.

Klein believes that the odontoblast forms the matrix only, whilst the dentinal fibrils are processes continued up between the odontoblasts from a subjacent layer of stellate cells.

Robin and Magitot formerly held that the dentine matrix was formed by the transformation of the odontoblast cells, but that the tubes were *interspaces* between these latter, not corresponding with the axes of the cells.

Baume (Odontologische Fortschungen) holds that the odontoblast secrete a material which calcifies, rather than that they are

themselves converted, and there are some appearances which are still unexplained. Mr. Mummery has shown to me sections of teeth with the pulps *in situ*, which had been prepared by impregnation with previously hardened Canada balsam ; in these there appears to be something in the pulp like a connective tissue stroma—something which reminds one of the connective tissue which calcifies into Sharpey's fibres in bone—adherent to the inner surface of the dentine. This, as well as some appearances after maceration in glycerine. described by Mr. Bennett (Odontolog. Soc. Transac., 1888), are as yet not fully explained, nor is it clear how far they may be due to methods used in the preparation of the specimens.

But it would appear that there must be some material of appreciable thickness upon the inner or forming surface of the dentine which is not as yet fully calcified. and perhaps not in other respects as yet structurally or chemically quite identical with the matrix even when this latter is decalcified (cf. Fig. 78), but which is on its way towards conversion into dentine matrix.

And it has been suggested (Hopewell Smith, Dental Record, Aug. 1889), that the function of the odontoblasts is purely sensory, a comparison being drawn between them and the ganglion cells of the spinal cord, and that the work of elaboration of dentine matrix, &c., is done by smaller and less specialised cells which lie more deeply in the pulp, just below the odontoblast layer.

Comparative anatomy furnishes evidence against the acceptance of such a view, as many vaso-dentines which contain no tube system, and so no dentinal fibrils, are yet formed apparently by the agency of a layer of cells corresponding in most features with the odontoblasts of other creatures.

Whilst the view advocated in the body of the text is that which appears to me to be the most probable, it cannot be said that the question of dentine calcification is finally and completely settled : there still remains room for doubt and for conjecture, so that no dogmatic statements can be laid down with safety.

The thinnest layer of dentine, such as may be found at the edges of the dentine cap, is soft and elastic, and so transparent as to appear structureless. Where it has attained a somewhat greater thickness, globules begin to appear in it, which are small in the thinner, and larger in the thicker portion of the dentine cap. As they are actually in the substance of the cap, their growth and coalescence obviously go on without any very immediate relation to the cells of the pulp ; in point of fact, a process strictly analogous to that demonstrated by Mr. Rainie and Professor

Harting (see page 187), is going on. Thus in the formation of the first skin of dentine, a stage of metamorphosis preparatory to impregnation with calcareous salts distinctly precedes that full impregnation, which is marked by the occurrence of globules and their subsequent coalescence. The occurrence of these globular forms and consequent large interglobular spaces, in the deeper parts of adult dentine, is therefore an evidence of arrest of development rather than of any otherwise abnormal condition.

When the formation of the dentine and enamel has gone on to the extent of the crown of the tooth having attained its full length, the reproduction of new formative pulp (in teeth of limited growth) takes place only over a contracted area, so that a neck, and finally one or more roots, are the result of its conversion into tooth substance. In teeth of constant growth, however, no such narrowing of the formative pulp takes place, but the additions to the base of the tooth are of constant, or ever-increasing dimensions, as is the case of some tusks, which are thus of conical form.

It is said that the number of roots which would have been developed at the base of a particular dentine organ may be inferred from the vessels, *i.e.*, that in a single rooted tooth the vessels would, even at an early period, form a single fasciculus, in a double rooted one similarly they would be arranged in two bundles, so that the ultimate formative activity will be exercised around one, two, or three centres of nutrition. I am not however able, from my own observations, to throw any light upon this matter.

THE CALCIFICATION OF VASO-DENTINE.

During the conversion of the membrana eboris into ordinary hard unvascular dentine the vessels of the formative pulp recede, so that, whilst at all stages a capillary plexus

is to be found just below the odontoblast layer, no vessels are to be found amongst the cells which constitute it.

Nevertheless a moment's reflection will show that (except in the earliest stages, before any dentine is formed) the plexus must at a prior time have occupied the place now taken possession of by the inward marching odontoblasts and dentine.

But in the calcification of a formative pulp into vaso-dentine this recession of its vessels before the advancing border of calcification does not take place; the whole vascular network of the papilla remains and continues to carry blood circulating through it, even after calcification has crept up to and around it.

So that, if we imagine a vascular papilla to have its stroma suddenly petrified whilst its circulation went on all the same, we should have something like a vaso-dentine.

Just as in hard dentine, the odontoblast layer is distinctly marked off from the rest of the dentine organ, and the dentine is wholly derived from its conversion into calcified material, so that the difference between vaso-dentine and hard dentine is not one of a very fundamental character.

Indeed as we have seen (page 92), the same formative pulp, the same odontoblast layer, is able at one time to form hard tubular dentine, at another vaso-dentine. All, therefore, that has been before said of the calcification of odontoblasts will apply equally to those of a vaso-dentine pulp, save only that in the most typical tissue of this latter kind each cell calcifies solidly, and does not leave the axial portion soft, to remain as a dentinal fibril.

Of the development of Plicidentine nothing more need be said, as it presents no peculiarities which are not the obvious result of the folding of the surface of its formative pulp.

THE CALCIFICATION OF OSTEO-DENTINE.

With the exception of the thin external layers (see Fig. 48), which are developed from a superficial layer of not very highly specialised cells, osteo-dentine is built up in a manner fundamentally different from that in which hard dentine, plicidentine, and vaso-dentine, are constructed.

For it is not, like these, a surface formation; it is not laid down in a regular manner upon the exterior of a pulp, and it has no relation to an odontoblast layer, if we except perhaps, its thin exterior shell.

So soon as this has been formed, its inner surface becomes roughened by trabeculæ shooting inwards into the substance of the pulp, which speedily becomes traversed completely by them, as well as by the connective tissue bundles which are continuous with them. Thus the pulp, being pierced through in every direction by these ingrowths, cannot be withdrawn, like the pulp of a hard or of a vaso-dentine tooth, from the interior of the dentine cap. Osteoblasts clothe, like an epithelium, the trabeculæ and the connective tissue fibres attached to them, and by the calcification of these the osteodentine is formed.

The process is exactly like the calcification of any membrane bone, and the connective tissue bundles remind one of those which are believed to be the occasion of the formation of Sharpey's fibres in bone. In the case of teeth which are going to be anchylosed to the subjacent bone, these fibres run continuously from the interior of the dentine cap down to the bone, and calcification in and around them binds the two inseparably together.

It is interesting to note, especially in connection with the fact that some observers believe Sharpey's fibres to be elastic, that the hinged teeth of the pike (see Fig. 90) owe their power of resilience entirely to the elasticity of these connective tissue bundles, which do not become completely

calcified; although at an early stage it would be quite impossible to say whether a particular tooth under observation was going to be anchylosed, or to be a hinged tooth tied down by elastic strings.

The Calcification of Cementum.—Just as is the case with bones elsewhere in the body, cementum may perhaps be formed in two distinct ways, by membranous ossification, and by ossification in a fibro-cartilage, the former method obtaining upon the roots of teeth, and the latter upon those crowns where the cement organ described by Magitot exists.

At the time when the crown of a tooth appears through the gum, it alone is complete, and the root has yet to be calcified; as each portion of dentine of the root is completed, it is coated with a closely adherent vascular membrane which is in fact the follicle wall, and which is to become, when the cement is formed, the alveolo-dental periosteum.

The inner or dentinal face of this membrane presents a layer of large cells, the osteoblasts of Gegenbaur, and it is by their calcification that bone or cementum is directly formed. These osteoblasts are themselves a special development where bone is about to be manufactured, as is clearly explained in the following extract from a paper by my father and the late Mr. De Morgan, who termed them osteal cells:—

"Here (towards the bone) in the place of cells with elongated processes, or cells arranged in fibre-like lines, we find cells aggregated into a mass, and so closely packed as to leave little room for intermediate tissue. The cells appear to have increased in size at the cost of the processes which existed at an earlier stage, and formed a bond of union between them. *Everywhere about growing bone a careful examination will reveal cells attached to its surface, while the surface of the bone itself will present a series of similar bodies ossified.* To these we propose to give the name of osteal cells."

Externally to the osteoblast layer, but still very near to

the perfect cementum, lies a reticulum or network made up of forming connective tissue. The cells have largish round nuclei, and are each furnished with three or four homogeneous processes, so that the tissue, save in very thin sections, looks hopelessly confused from the interlacing of the cell processes. Many of these processes pass into, and are lost in the clear, structureless matrix of the already formed cementum; the functions which they perform in its development are not very apparent, but some of them appear to persist in it as Sharpey's fibres.

Externally to the fine-meshed net-work which has been well figured and described by Dr. Lionel Beale, the soft tissue surrounding the root partakes more of the character of ordinary fibrous tissue, and may be teased out into fibrils. The fibrous bands run mainly in a direction from the alveolus towards the tooth. Many of them pass through the whole thickness of the soft structures, extending from the bone of the alveolus to the cementum of the tooth, becoming lost at each extremity in the one tissue or other.

The osteoblasts form both matrix and bone corpuscles: in Professor Klein's words "each osteoblast by the peripheral portion of its cell substance gives origin to the osseous ground-substance, while the central protoplasm round the nucleus persists with the latter as the nucleated bone-cell. The bone-cell and the space in which it lies become branched. For a row of osteoblasts we then find a row of oblong or round territories, each composed of matrix, and in it a nucleated branched cell. The outlines of individual territories are gradually lost, and we have then a continuous osseous lamina, with its bone-cells. The ground substance is from the outset a network of fibrils; it is at first soft, but soon becomes impregnated with inorganic salts, the process commencing at the 'point of ossification.' The bone cells, with their processes, are situated in corresponding lacunæ and canaliculi, just as in the adult osseous substance."

Thus just as calcification in an enamel cell or in an odontoblast commences upon its surface, and proceeds inwards till it has more or less completely pervaded it, so in the case of the osteoblast the deposition of calcareous salts proceeds from without inwards. To use a rough comparison, we might imagine a calcifying osteoblast as like an egg-shell, the central cavity of which was being gradually obliterated by the addition of successive layers on its interior (it is not to be understood that any such lamination is to be detected in an individual osteoblast). In a certain number of osteoblasts this process of calcification does not proceed with such regularity as to obliterate their centres, and at the

FIG. 78 (1).

same time to fuse together their exteriors, but as it progresses with some degree of irregularity towards the centre, tracks of uncalcified matrix are left, and finally it stops short of obliterating the central portion of the cell. Although for the purpose of description I have spoken of the centre of the osteoblast cell as a 'space,' of course it is not hollow, but consists of uncalcified matrix, and in this situation lies the nucleus of the cell.

In carmine-stained preparations from the teeth of calves a round nucleus may sometimes be seen lying in the stellate

(1) Encapsuled lacunæ.

"lacuna;" the nucleus soon disappears, and plays no active part in determining the form of the lacuna. The nucleus may also be seen in the developing bones of human fœtuses, and, though this is difficult to understand, the traces of the nucleus seem to be beautifully preserved in the lacunæ of a supposed Pterodactyle bone from the Wealden, a section from which was figured by my father in the paper referred to. Exactly as calcification, advancing with irregularity in the interior of an individual cell, fails to render it homogeneous by pervading its whole substance, so it may fail so completely to unite contiguous cells as to obliterate their contours. A lacuna, surrounded by such a contour line, mapping the limits of the original cell, or cluster of cells, is what is termed an "encapsuled lacuna."

That which determines the formation of a lacuna, or an encapsuled lacuna, at any particular spot, is unknown: all that can certainly be said upon the subject is embodied in the following extract from the paper by my father and Mr. De Morgan, above alluded to:—"We see the boundary of the original lacunal cells only in those cases where the lacunæ have but few, or are entirely devoid of canaliculi. It would appear to be a law, to which there are few, if any, exceptions, that when anastomosis is established between adjoining lacunæ, the lacunal cells blend with the contiguous parts, and are no longer recognisable as distinct bodies."

According to Kölliker, the cementum is first deposited in isolated scales, which coalesce with one another, rather than in a continuous sheet. In the teeth of the Primates, the Carnivora, Insectivora, &c., the cementum, at least in any appreciable thickness, is confined to the roots of the teeth. Various reasons, however, exist, for regarding Nasmyth's membrane as an exceedingly thin layer of cement, which have been entered into in the section relating to that structure, and need not be recapitulated here. It will

suffice to say, that it appears to be one of those structures midway betwixt full calcification and full vitality, and shares with such substances the power of resistance to chemical reagents which characterises them.

M. Magitot states that the calcification of the cartilaginous cement organ of Herbivora differs in no respect from that of other cartilages, but in his description he merely states that patches of calcification appear here and there in the deepest portion of the organ, coalesce, and come to invade its entire thickness; and further that the cement at the period of eruption is constituted of "osteoplasts" regularly grouped round vascular canals, and included in a ground substance finely striated. (*Journal de l'anatomie*, 1881, p. 32.) Where intra-cartilaginous ossifications occur elsewhere in the body a temporary bone is formed by the calcification of the cartilage matrix, which is subsequently absorbed and swept away, as marrow-containing channels appear in it, and bore their way through it, substituting for the calcified cartilage a bone developed from osteoblasts, and ultimately all remains of the calcified cartilage or temporary bone disappear. Thus all bone whether developed in cartilage or in membrane is formed alike, the calcified cartilage merely forming a temporary framework or scaffolding, in and amongst which the bone is formed from osteoblasts. But M. Magitot does not describe in much detail this calcification of cartilage and subsequent removal to give place to an osteoblast-derived bone, though he speaks of the cartilaginous cement organ as a transitory or temporary structure.

Membrana Preformativa.—To the student of dental development, few things are more perplexing than the conflicting statements which he reads in various works as to the nature and position of the Membrana preformativa, of which I have hitherto studiously avoided all description ; while it is not encouraging, after having mastered with difficulty some one description of its character, to find that

many of the most recent authors altogether deny its existence. I will endeavour, therefore, so far as I am able, although not myself believing in its presence, to put the matter in a clearer light, and to point out wherein lie the discrepancies of statement.

According to the older theories of tooth development, under the thrall of which most authors have written, the tooth germ was in the first instance a free, uncovered papilla of the mucous membrane, which subsequently sank in and became encapsulated, &c., &c. (see page 121). Moreover, it was taught by the older histologists that fine homogeneous "basement membranes" were to be found in a great variety of situations, amongst others beneath the epithelium of the mucous membrane, and that these were of (physiologically) much importance, inasmuch as they formed defining limits, through which structures did not pass. As a necessary consequence of these views, it was assumed as a matter of course that the "dentine papilla" must be covered over by a "basement membrane," or membrana preformativa.

Thus this membrane necessarily intervened between the enamel organ and the dentine papilla, and hence gave rise to difficulties in the understanding of the calcifying process. Henle considered that evidences of its presence speedily became lost, but that ossification proceeded in opposite directions upon the two sides of this membrane: from within outwards in the case of the enamel, from without inwards in the case of the dentine.

Prof. Huxley, starting on the same hypothesis as to its position, namely, that it was between the enamel organ and the dentine papilla, came to a different conclusion as to its after fate; relying upon the fact that a continuous sheet of tissue or membrane can be raised from the surface of the developing enamel (see page 164), he concluded that this was the original membrana preformativa, that it afterwards became the Nasmyth's membrane, and that enamel was

developed without the direct participation of the enamel organ, seeing that a membrane separated the two. My reason for doubting the correctness of these conclusions has been there given; the membrane so demonstrable is, I believe, artificial, and does not represent any naturally existing structure.

Kölliker strongly affirms the existence of the membrana preformativa, and in the older edition of his Histology, held that it became converted into Nasmyth's membrane; although he now gives a different explanation of the origin of Nasmyth's membrane, I have not found a definite statement as to his recent views of the ultimate fate of the membrana preformativa.

We have thus three situations assigned to the membrane covering the dentine papilla, or membrana preformativa.

(i.) Between the dentine and the enamel (Henle).

(ii.) Between the enamel and the enamel organ, or outside the enamel (Huxley).

(iii.) Between the dentine and the pulp (several writers of less authority).

We come next to those writers who deny its existence altogether, explaining on other grounds the appearances observed.

Markusen believed that it was nothing more than the part of the papilla first ossified; and Dr. Lionel Beale definitely denies the existence of a membrane in any one of the three situations above detailed, as do also Hertz, Wenzel, and Waldeyer.

Messrs. Robin and Magitot have offered a plausible explanation of the appearance of a limiting membrane over the pulp, which is briefly this: the formative pulp is rich in a clear substance of gelatinous consistency (which in fact forms its chief bulk), and which reminds the observer of the tissue contained in an umbilical cord. This is some-

what more dense towards the surface, where it forms a matrix for the odontoblasts and projects beyond them, so as to look, in section or at a thin edge, like a sort of varnish to the papilla. From its greater density near the surface, it may become corrugated, and so look like a folded or torn membrane. I am quite inclined to agree with the foregoing explanation.

I am inclined to think, that but for the erroneous theories that the dentine germ originated as a free papilla on the surface, which would according to the prevalent view have been necessarily invested by a basement membrane, we should never have heard of a membrana preformativa. At all events it is difficult to imagine that such a membrane exists upon papilla formed at such a great distance from the surface as those of the snake or the lizard (Figs. 62 and 63); and if there be such a membrane, it must be a secondary development upon the surface of the mass of cells which primarily constitute the rudiment of the dentine papilla, and in that case is not a part of the general basement membrane of the oral mucous membrane; or else it must have been carried above as a sort of *cul de sac* in front of the inward growing process of epithelium, to which in that case it would belong rather than to the dentine germ. Neither of these suppositions commend themselves as probable; and a still greater obstacle to the acceptance of a membrane in this position is afforded by the structure of Marsupial teeth (see Fig. 24), in which the membrane would be everywhere perforated by the soft contents of the dentine and enamel tubes.

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CHAPTER V.

THE DEVELOPMENT OF THE JAWS—THE ERUPTION AND THE ATTACHMENT OF THE TEETH.

At an early period in the development of the embryo there is a single primitive buccal cavity, which is subsequently divided into a nasal and an oral cavity by the palatine plates growing horizontally across it; the pharynx behind the hinder end of the primitive buccal cavity remains undivided. Both upper and lower jaws make their appearance about the twentieth day as little buds from the first visceral arch, and grow inwards towards the middle line: those which form the lower jaw reach to the middle and there coalesce, those for the upper jaw stop short, and the gap left between them is filled by a double downward sprouting process from the forehead, which afterwards forms the intermaxillary bones. A failure in the coalescence of the maxillary processes with this intermaxillary process, on one or both sides, results in a single or double hare-lip.

In the lower jaw or mandibular processes there appears, about the end of the first month, a dense cord of cartilaginous consistence, Meckel's cartilage, which seems to serve as a scaffolding, giving form and consistency to the lower jaw prior to the occurrence of calcification. Meckel's cartilage, formed as two distinct halves, soon unites in the middle, and then forms a continuous curved bar, the hinder ends of which reach up to the tympanum.

About the fortieth day a centre of ossification appears in

the mandibular process, which, spreading rapidly, soon forms a slight osseous jaw outside Meckel's cartilage, which is not however in any way implicated in it, and very soon begins to waste away, so that by the end of the sixth month it has disappeared: that end of it alone which extended up to the tympanum does not so waste away, but becomes ossified into the malleus. There, are, however, observers who hold that in some animals, at all events, Meckel's cartilage plays a more active part in ossification of the jaw.

The development of the lower jaw has been accurately described by Mr. Bland Sutton (Trans. Odonto. Soc., 1883). After the appearance of Meckel's cartilage, a centre of calcification appears at a point below the future mental foramen, to which the name of the dentary centre is given; then centres appear for the condyle, the coronoid process, the angle, and, at the chin, a mento-meckelian centre.

An osseous network soon connects these, and a splenial calcification appears as a ledge of bone on the inner side of the forming jaw immediately above Meckel's cartilage and the inferior dental nerve. Upon this splenial portion the tooth germs stand "like flasks upon a shelf," then subsequently, as Meckel's cartilage atrophies, the splenial extends downwards to fuse with the dentary, and so cuts off the mylohyoid branch of the inferior dental nerve, which branch runs along the groove once occupied by Meckel's cartilage.

It will thus be seen that the centres described by Mr. Bland Sutton correspond pretty closely with the several bones which, though remaining distinct, together go to make up the mandible in Sauropsida; namely, the articular, angular, dentary, and splenial bones.

In the upper jaw the suture separating the intermaxillary from the maxillary bones becomes obliterated very early on the exterior surface, but it remains long distinguishable on the palatine aspect of the bones.

According to Albrecht the intermaxillary bones are deve-

loped each from two centres, and for a time there are traces of suture separating these, so that he divides the inter-maxillary bone into an "endognathion" and an "exognathion."

The later changes which are undergone by the jaws during the development, eruption, and loss of the teeth, have long engaged the attention of anatomists, and amongst others of Hunter, who was the first to arrive at a tolerably correct appreciation of the process. In the first edition of my father's "Dental Surgery," the results of a very extensive series of observations carried out upon maxillæ collected by himself, were detailed, confirming in the main Hunter's conclusions, but adding many new points to our knowledge; and from this work I have borrowed largely in the present chapter. Professor Humphrey, who had overlooked these descriptions, which were never published in any other form than as an introduction to the "Dental Surgery," instituted a series of experiments upon growing animals, which tended towards the same conclusions.

As a means of giving the student a guide in his reading of the following pages, and a clue to the results towards which he is being led, a preliminary statement, which does not pretend to scientific accuracy, may perhaps be useful; while the description given will relate for the most part to the lower jaw, because its isolated position, bringing it into relation with fewer other bones, renders it more easy to study; not that any difference of principle underlies the growth of the upper jaw. The different parts of the lower jaw answer for different purposes; one division of its body having a very close and intimate relation with the teeth, the other serving a distinct purpose, and being only secondarily connected with the teeth.

The alveolar portion of the jaw, that which lies above the level of the inferior dental canal, is developed around the milk teeth: when they are lost, it disappears, to be re-formed

again for the second set of teeth, and is finally wholly removed after the loss of the teeth in old age.

The portion of jaw below this line, which is essential to deglutition and respiration, is late in acquiring any considerable development. Once formed it is never removed, save that when in advanced old age the muscles of mastication are no longer in full use, it becomes, to a slight extent only, wasted.

In order to understand the drift of the following description, it is essential to keep in view the different life histories of those two parts of the jaw just alluded to.

In an early fœtus, long before the necessity for respiratory movement or deglutition has become imminent, a thin lamina of bone has begun to be formed beneath the tooth germs, forming, as it were, a semicircular gutter running round the jaw, in which the developing tooth sacs are lodged. The thin gutter of bone thus formed is above and outside Meckel's cartilage, and intervenes between the rudimentary inferior maxillary vessels and nerves, and the teeth. The sides of the bony furrow rise as high as the top of the tooth germs, but they do not arch over and cover them in, in such manner as the permanent tooth germs are arched in, for the long furrow is widely open at the top.

Passing on to the condition of the mandibles at the time of birth, the two halves are as yet not anchylosed, but are united only by fibro-cartilage. "The alveolar margins are deeply indented with large open crypts, more or less perfectly formed. The depth of these bony cells is only sufficient to contain the developing teeth and tooth pulps, the former rising to the level of the alveolar margins of the jaws. At this period the crypts or aveoli are not arranged in a perfectly uniform line, nor are they all equally complete. The septa, which divide into a series of cells that which at an earlier age was but a continuous groove, are less perfect at the back than at the front part of the mouth. The

alveoli of the central incisors of the upper and the lower jaws are a little larger within than at the orifice, and this

FIG. 79 [1].

[1] Upper and lower jaws of a nine months fœtus, the teeth having been removed from the jaws on one side to show the extent to which they are calcified at this period. (Two-thirds life size.) *a.* Alveoli of lateral incisors. *b.* Alveoli of canines. *c.* Alveoli of second temporary and first permanent molars. A bristle has been passed through the inferior dental canal.

difference is made still greater by a depression upon the lingual wall of each for the reception of the pulp of the corresponding permanent tooth. They are divided from the crypts of the lateral incisors by a septum which runs obliquely backwards and inwards towards the median line. The sockets for the lateral incisors occupy a position slightly posterior to those for the central teeth, and are divided from the canine alveoli by a septum which proceeds obliquely backwards, and in the lower jaw, as regards the median line of the mouth, outwards. By the arrangement of these divisions, the alveoli of the central incisors are rendered broader in front than behind, and the relative dimensions of the sockets of the lateral teeth are reversed, as shown in Fig. 79. The crypts of the canine teeth are placed a little anteriorly to those of the laterals, and nearly in a line with those of the central incisors, giving to the jaws a somewhat flattened anterior aspect."

While the main bulk of the lower jaw is made up by the alveoli of the teeth, in the upper jaw the alveoli descend but little below the level of the palatal plates, though the sockets are tolerably deep. The antrum as a special distinct cavity cannot be said to exist, being merely represented by a depression upon the wall of the nasal cavity, the alveolar cavities therefore being separated only by a thin plate of bone from the orbits.

The figure represents also the extent to which calcification has advanced in the various teeth.

A full half of the length of the crowns of the central incisors, about half that of the laterals, and the tips only of the canines aro calcified; the first temporary molars are complete as to their masticating surfaces; the second temporary molars have their cusps more or less irregularly united, in many specimens the four cusps being united into a ring of dentine, the dentine in the central depression of the crown not being yet formed. During the formation of

the permanent teeth, very similar relations exist between the amount of calcification in the incisors and canines ; thus when, as sometimes happens, the development of the teeth proceeds very imperfectly up to a certain date, and then changes for the better, it may be that the lower half of the crown of the central incisor, somewhat less of the lateral, and the extreme tip of the canine will be honeycombed, while the remainder of the tooth will be perfect, thus perpetuating an evidence of the stages to which each of these teeth had at that particular period attained.

Having noted in some detail the characters of the jaws of a nine months fœtus, we may pass on to the consideration of those changes which precede the cutting of the deciduous teeth. A general increase in size takes place, new bone being developed at all those points where the maxillæ are connected by soft tissue with other bones, as well as from their own periosteum. But the increase in dimensions does not take place in all directions equally, so that material changes of form result.

In correspondence with the elongation of the tooth sacs, the alveoli become increased in depth, and their edges circle inwards over the tooth sacs ; active development of bone takes place in the sutures uniting the two halves of the jaws to one another, which is compensated by the inclination inwards of the alveoli of the central incisors. In the lower jaw the articular process, at first hardly raised above the level of the alveolar border, rises rapidly up, the direction of the ramus at first remaining oblique, though the angle of the jaw becomes developed as a stout process for the attachment of muscles. At the age of six months the symphysis is still well marked, and the mental prominence first becomes noticeable.

An additional bony crypt for the first permanent molar has also appeared, though its separation from that of the second temporary molar, from which it was at first in no way

distinct, is yet incomplete, especially in the lower jaw. In the upper jaw the first permanent molar crypt has no posterior wall; bony cells for the permanent central incisors are well marked, but those for the laterals are mere deep pits in the palatine wall of the crypts of the temporary teeth.

FIG. 80 (1).

At the age of eight months, or thereabouts, the process of the eruption of the teeth, or "teething," has fairly set in: anchylosis has taken place at the symphysis of the lower jaw, the mental prominence is well marked, and in the upper jaw the antrum has become a deep depression, extending under the inner two-thirds of the orbit.

Postponing for the moment the consideration of the eruption of the teeth, in order to follow up the growth of the jaws, it becomes necessary to take some fixed points as standards from which to measure the relative alteration of various portions of the bone. In most bones, processes for the attachment of muscles would be very unsuitable for the purpose, because they would alter with the general alteration in the dimensions of the bone: thus a process situated at a point one-third distant from the articular extremity of a long bone, will still be found one-third distant from the end, though the bone has doubled in length. The four little tubercles which give attachment to the genio-hyo-glossus and genio-hyoid muscles are not, however, open to these objections, as they are already, so to speak, at the end of the

(1) Lower jaw of a nine-months fœtus.

bone, or, at least, of each half of it; and their general correspondence in level with the inferior dental canal, which can hardly be imagined to undergo much alteration, indicates that their position is tolerably constant.

The points selected as landmarks are then, the spinæ mentales, the inferior dental canal and its orifice, and the mental foramen. The mental foramen itself does undergo slight change in position, but this change can easily be estimated, and may as well at once be mentioned. As the jaw undergoes increase in size, large additions are made to its surface by deposition of bone from the periosteum, necessarily lengthening the canal. The additions to the canal do not, however, take place quite in the line of its original course, but in this added portion it is bent a little outwards and upwards. If we rasp off the bone of an adult jaw down to the level of this bend, a process which nature in great part performs for us in an aged jaw, or if instead we make due allowance for the alteration, the mental foramen becomes an available fixed point for measurement.

The mental foramen, which undergoes most of its total change of position within a few months after birth, comes to correspond with the centre of the socket of the first temporary molar; later on it corresponds with the root of the first bicuspid, which is thus shown to succeed, in exact vertical position, the first temporary molar.

On the inner surface of the jaw the tubercles for the attachment of the genio-hyo-glossus and genio-hyoid muscles are in the fœtus, opposite to, and very little below, the base of the alveoli of the central incisors, a position which they afterwards hold with regard to the permanent incisors. The upper of the two pairs of processes are about at the same general level as the mental foramen.

The general result arrived at by measurements taken from these fixed points is that the alveolar arch occupied by the teeth which have had deciduous predecessors, namely the

incisors, canines, and bicuspids, correspond very closely with the whole alveolar arch of the child in whom the temporary dentition is complete; and that the differences which do exist are referable, not to any fundamental alteration in form or interstitial growth, but to mere addition to its exterior surface. Or more briefly, that the front twenty of the permanent succeed vertically to the places of the temporary teeth, the increase in the size of the jaw in an adult being due to additions at the back, in the situation of the true molars, and to other points on the surface.

If measurements be taken across between the inner plates of the alveoli on either side at the points where they are joined by the septa between the first and second temporary molars, and at about the level of the genio-hyo-glossus tubercles, it will be found that the increase is slight, if any, notwithstanding that in other dimensions there is a very great difference between the jaws of a nine-months fœtus and of a nine-months child.

Again, if an imaginary line be stretched across between these two points, and from its centre a line be drawn forwards to the spina mentalis in the same two jaws, this will be found to differ but little in length in the two specimens.

But, if instead of measuring to the spina mentalis, the line had been carried to the anterior alveolar plate, a great difference would have been observable; in point of fact, contemporaneously with the development of the crypts of the permanent teeth inside them, the temporary teeth and their outer alveolar plates are slowly pushed outwards, a process, the results of which we see in the separation which comes about between each one of the temporary teeth, prior to their being shed, where the process of dentition is being carried on in a perfectly normal manner.

Measurements taken for the sake of comparing adult jaws with those of an eight-months child, give closely similar

results, which I have endeavoured to roughly embody in the accompanying figures.

In these it is shown that the increase in the dimensions

Fig. 81 [1].

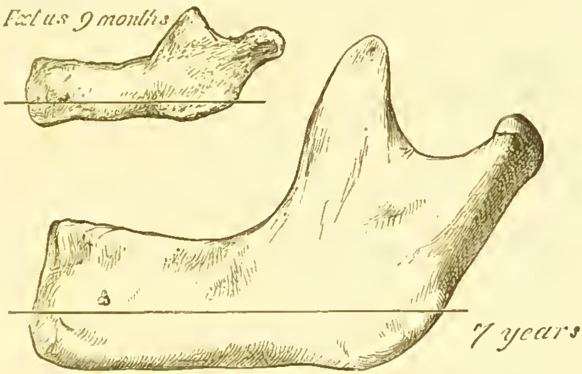
of the jaw has taken place in two directions: by prolongation backwards of its cornua concomitantly with the addition at the back of the series of teeth of the true molars, which follow one another at considerable intervals; and by additions to its exterior surface by which it is thickened and strengthened. The study of the growth of the jaw in vertical depth is also very instructive. We find that, as has already been mentioned, the history of that part of the jaw which lies below the inferior dental canal is very different from that which lies above. From the time of birth to that

[1] Diagram representing a jaw of a nine-months fœtus, superimposed upon an adult jaw, to show in what directions increase has taken place.

at which the temporary teeth begin to be cut, the jaw below that line has been making steady but slow progress in vertical depth; the alveoli, above that line, have been far more active but far more intermittent in their development.

Again, passing from the nine-months fœtus to the seven-

FIG. 82 (1).



years-old child, in whom the temporary dentition is complete, the framework of the jaw below our imaginary line has attained to a depth almost equal to that which it is seen to have in an adult; in the adult again it corresponds pretty well with that in an aged jaw. The alveolar portion, however, is far deeper in the adult than in the child (this difference is not sufficiently well marked in the figure), and in fact constitutes almost the whole increase in vertical dimensions down the passage from the child's to the adult's form of the jaw.

In the lower jaw we may take it as proven that the basal portion has little relation to the development of the teeth, but that the alveolar, or upper, portion is in entire and absolute dependence upon them, a point to

(1) Lower jaw. The horizontal line marks the level of the inferior dental canal.

which I shall again return in speaking of the eruption of the teeth.

It remains to speak in some further detail of the

Fig. 83 (1).

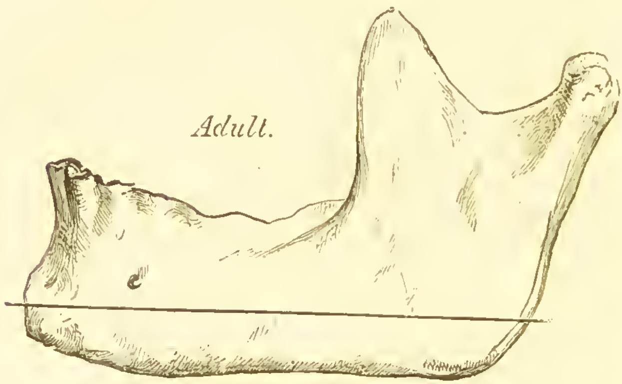
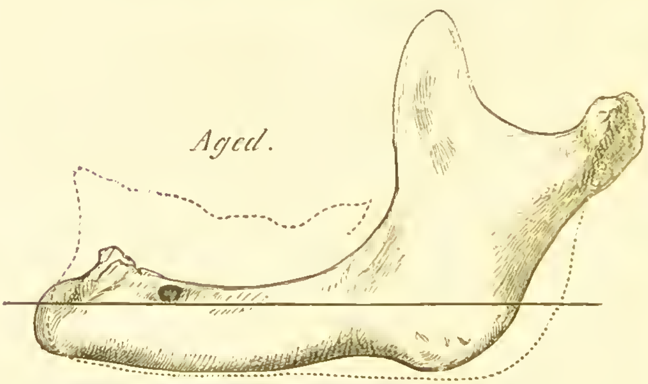


Fig. 84 (2).



precise means by which the enlargement of the jaw is effected.

To a slight extent there is formation of bone going on at the symphysis, prior to the complete anchylosis taking

(1) Lower jaw of an adult.
(2) Lower jaw of an aged person, the dotted lines indicating the outline of the parts removed by absorption, as the jaw assumes the form characteristic of advanced age.

place: the share taken by this in increasing the size of the jaw would, however, appear to be but small, after the termination of the intra-uterine period. Additions to the surface, at the edges of the alveoli and at the base of the jaw, are continually going on, and bring about that addition to the exterior already noticed.

But the main increase in the size of the jaw has been in the direction of backward elongation; in this, as Kölliker first pointed out, the thick articular cartilage plays an important part. The manner in which the jaw is formed might also be described as wasteful; a very large amount of bone is formed which is subsequently, at no distant date, removed again by absorption; or we might compare it to a modelling process, in which thick, comparatively shapeless masses, are dabbed on to be trimmed and pared down into form.

To bring it more clearly home to the student's mind, if all the bone ever formed were to remain, the coronoid process would extend from the condyle to the region of the first bicuspid, and all the teeth behind that would be buried in its base: there would be no "neck" beneath the condyle, but the internal oblique line would be a thick bar, corresponding in width with the condyle. It is necessary to fully realise that the articular surface with its cartilage has successively occupied every spot along this line; and as it progresses backwards by the deposition of fresh bone in its cartilage, it has been followed up by the process of absorption removing all that was redundant.

On the outer surface of the jaw we can frequently discern a slight ridge, extending a short distance from the head of the bone; but if the prominence were preserved on the inner surface, the inferior dental artery and nerve would be turned out of their course. We have thus a speedy removal of the newly-formed bone, so that a concavity lies immediately on the inner side of the condyle; and microscopic

examination of the bone at this point shows that the lacunæ of Howship, those characteristic evidences of absorption, abundantly cover its surface, showing that here at least absorption is most actively going on.

In the same way the coronoid process, beneath the base of which the first, second, and third molars have successively been formed, has moved backwards by absorption acting on its anterior, and deposition on its posterior surfaces.

The periosteum covering the back of the jaw is also active in forming the angle and the parts thereabouts.

It is worth while to add that the direction of growth in young jaws is marked by a series of minute ridges; in like manner the characteristic marks of absorption are to be found about the neck of the condyle, and the front of the coronoid process, and those of active addition about the posterior border, so that the above statements rest upon a basis of observation, and are not merely theoretical. Two cases of arrested development of the jaw ("Dental Surgery," p. 108) lend a species of experimental proof to the theory of the formation and growth of the jaw above given.

There are authors, however, who maintain that the growth of the jaws is not merely a backward elongation of the cornua, together with additions to the external surface, but that an "interstitial growth" takes place.

Wedl inclines to this latter view, and the question cannot, I think, be held to be absolutely settled. Although it is difficult to form any definite conception of interstitial growth in a tissue so dense and unyielding as bone, so that the doctrines promulgated in the foregoing pages have the support of *a priori* probability, there are some rather paradoxical facts to be met with in comparative odontology. Nevertheless, there can be no doubt, that backward elongation as teeth are successively added, &c., is sufficiently near the truth in the case of human and most mammalian jaws for practical purposes.

It remains to notice the changes in form which the ascending ramus and the angle of the jaw undergo. In the fœtus the ramus is but little out of the line of the body of the jaw, and the condyle little raised above the alveolar border.

Gradually the line of development, as is indicated even in the adult jaw by the course of the inferior dental canal, takes a more upward direction; copious additions of bone are made on the posterior border and about the angle, so that in an adult the ramus ascends nearly at right angles to the body of the jaw.

In old age, concomitantly with the diminution of muscular energy, the bone about the angle wastes, so that once more the ramus appears to meet the body at an obtuse angle. But all the changes which mark an aged jaw are the simple results of a superficial and not an interstitial absorption, corresponding with a wasting of the muscles, of the pterygoid plates of the sphenoid bone, &c.

ERUPTION OF THE TEETH.

The mechanism by which teeth, at the date of eruption, are pushed upwards into place, is far from being perfectly understood. The simplest theory would appear to be that they rise up, in consequence of the addition of dentine to their base; in fact that their eruption is due to the elongation of their fangs.

Various very strong objections have been brought forward, clearly proving that this cause is quite inadequate to explain all that may be observed. In the first place, teeth with very stunted roots—which may be practically said to have no root—are often erupted. Again, a tooth may have the whole length of its roots completed, and yet remain buried in the jaw through half a person's life, and then, late in life,

be erupted. Moreover, when a healthy normal tooth is being erupted, the distance travelled by its crown materially exceeds the amount of addition to the length of its roots which has gone on during the same time.

To turn to comparative anatomy, the tooth of a crocodile moves upwards, tooth pulp and all, obviously impelled by something different from mere elongation; and my own researches upon the development and succession of reptilian teeth clearly show that a force quite independent of increase in their length shifts the position of, and "erupts" successive teeth. But what the exact nature of the impulse may be, is an unsolved riddle: the explanations which I have read being, to my mind, less satisfying than the admission that we do not know.

Towards the eighth month of childhood the bony crypts which contain the temporary teeth in the front of the mouth begin to be removed. The process of absorption goes on with greater activity over the fronts of the crowns than over their apices, so that almost the whole outer wall of the alveoli is removed. At the back of the mouth the crypts still retain their inverted edges; indeed, development of the crypts is still going on in this part of the mouth.

When a tooth is about to be cut, very active absorption of its bony surroundings goes on, particularly on the anterior surface, the bone behind it being still required as forming part of the crypt of the developing successional tooth. But no sooner has the crown passed up through the very wide and free orifice so formed, than absorption gives place to deposition, and the bone rapidly developes so as to loosely embrace the neck of the tooth.

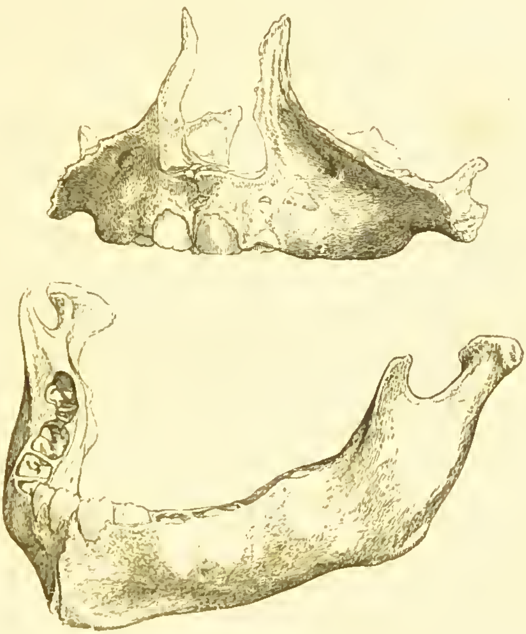
Additions to the margin of the alveoli keep pace with the gradual elongation of the roots of the teeth; as this is a moderately rapid process, the alveolar portion of the jaw increases in depth almost abruptly.

But it does not do so uniformly all over the mouth; if it

did, the teeth could only be closed at the back of the mouth, unless the rami elongated by an equally sudden accession of new bone.

The front teeth are erupted first, and the jaw deepens first in front: later on the back teeth come up and the jaw

FIG. 85 (1).



is deepened posteriorly; meanwhile the elongation of the rami has been going on slowly, but without interruption. Thus is brought about a condition of parts allowing of the whole series of teeth coming into their proper mutual antagonism.

It was pointed out by Trousseau that the eruption of the teeth is not a continuous process, which, once commenced, is carried on without intermission to its completion, but that it

(1) Jaws of a male nine months old, in which the eruption of the teeth is just commencing.

is interrupted by periods of repose. The teeth are, according to his statement, cut in groups; the eruption of the teeth of each group being rapid, and being succeeded by a complete cessation of the process. Individual variations are numerous; the following may be taken as an approximation to the truth:—

The lower centrals are erupted at an age ranging from six to nine months; their eruption is rapid, and is completed in ten days or thereabouts; then follows a rest of two or three months.

Next come the four upper incisors; a rest of a few months; the lower laterals and the four first molars; then a rest of four or five months.

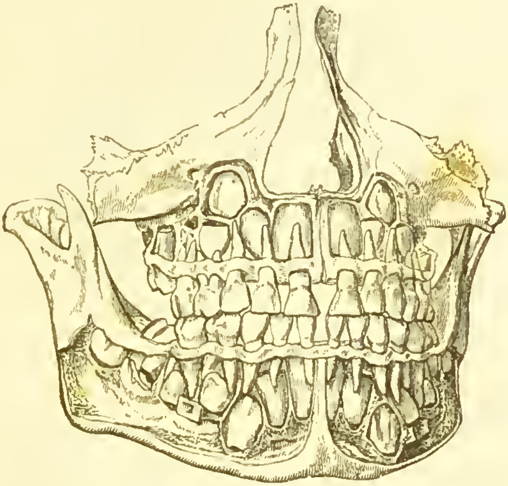
The canines are peculiar in being the only teeth of the temporary set which come down between teeth already in place. To this, as well as to the greater length of their root (though it is not quite clear what this has to do with it), Trousseau ascribes the great length of time which their eruption occupies, it taking two or three months for its completion. According to him, children suffer more severely from constitutional disturbance during the cutting of these teeth than that of any other, but Dr. West thinks that the eruption of the first molars causes the most suffering. It may also be noted that the canines during their development lie farther from the alveolar border than do the other teeth, so that they travel a greater distance; obviously, not merely from the elongation of the root, which is wholly inadequate to effect such a change in position.

The dates of the eruption of the milk teeth vary much, no two authors giving them alike; but the whole of the deciduous teeth are usually cut by the completion of the second year. Cases in which incisors have been erupted before birth are not very uncommon. At a time when the crowns of all the deciduous teeth have been fully erupted, their roots are still incomplete, and are widely open at their

basis, so that it is not till between the fourth and sixth years that the temporary set of teeth can be called absolutely complete.

At the sixth year, preparatory to the appearance of any

Fig. 86 ([1]).



of the permanent teeth, the temporary teeth may be observed to be slightly separated from each other; they have come to occupy a more anterior position, pushed forward, it may be, by the great increase in size of the crypt of the permanent teeth behind them. The general relation of these to the temporary teeth may be gathered from the accompanying figure, in which it will be noticed that the canines lie far above and altogether out of the line of the other teeth, and that a slight degree of overlapping of the edges of the permanent central and lateral incisors exists.

The bicuspids lie in bony cells which are embraced pretty closely by the roots of the temporary molars, and it hence

([1]) Normal well-formed jaws, from which the alveolar plate has been in great part removed, so as to expose the developing permanent teeth in their crypts in the jaws.

happens that extraction of the latter sometimes brings them away in their entirety.

The first permanent molars are erupted in a manner closely similar to that described as occurring with the temporary teeth; that is to say, their bony crypts become widely opened out by absorption, the crown passes out, and new bone is rapidly formed which embraces the neck, prior to any considerable length of root being formed.

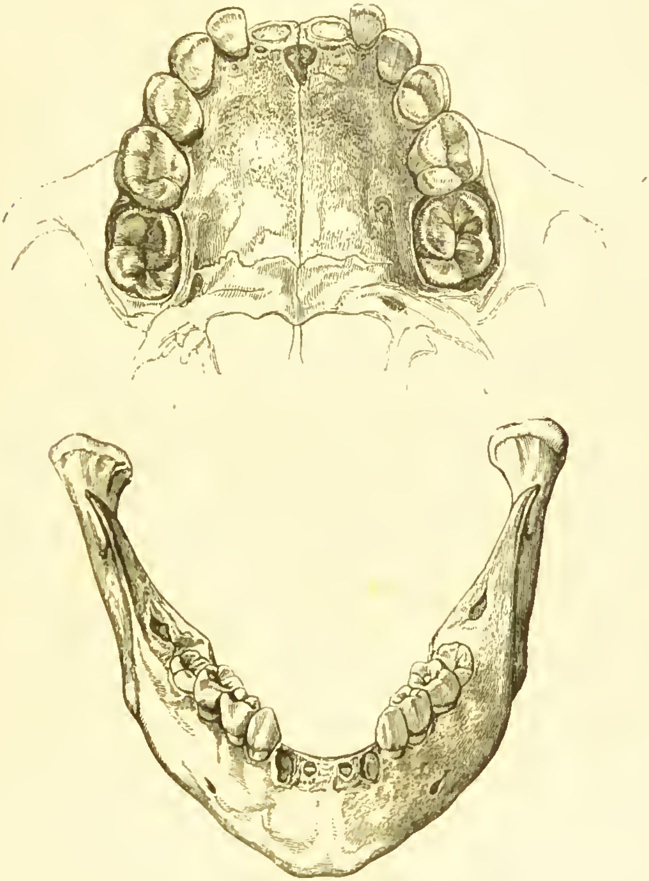
Last, then, follows the absorption of the root of the temporary teeth, a matter first accurately investigated by my father. The root at or near to its end, becomes excavated by shallow cup-shaped depressions; these deepen, coalesce, and thus gradually the whole is eaten away. Although absorption usually commences on that side of the root which is nearest to the successional tooth, it by no means invariably does so; it may be, and often is, attacked on the opposite side, and in many places at once.

The cementum is usually attacked first, but eventually dentine, and even enamel, come to be scooped out and removed by an extension of the process. That part of the dentine, however, which immediately surrounds the pulp appears to have more power of resistance than any other part of the tooth, and thus often persists for a time as a sort of hollow column. The absorption of the temporary teeth is absolutely independent of pressure; the varying position of the excavation has already been noticed, and it may be added that in many lower animals, for example, the frog or the crocodile, the growing tooth sac passes bodily into the excavation made before it in the base of the tooth which has preceded it, while if pressure had had any share in the matter the cells of its enamel organ, &c., must have inevitably been crushed and destroyed.

Again, when the absorption and shedding of the first teeth have taken place early, before their successors are ready to appear, perfect little sockets are formed behind the lost

temporary teeth, cutting them off from the permanent teeth destined to follow them. Absorption, too, may attack the roots of permanent teeth, which is another reason for regard-

FIG. 87 ([1]).



ing the process as not necessarily dependent upon the approach of a displacing tooth. Closely applied to the excavation produced by absorption is a mass of very vascular soft tissue, the so-called absorbent organ. The surface of

([1]) Jaws of a six-year-old child. In the upper jaw complete sockets are seen where the temporary incisors have been shed.

this is composed of very large peculiar-looking cells, bearing some little resemblance to those known as "myeloid cells," or the "giant cells" of recent authors. Microscopic examination of the excavated surface shows it to be covered with small hemispherical indentations, the "lacunæ of Howship," into each of which one of the giant cells fitted, and in which they may sometimes be seen *in situ*.

In what manner these giant cells, or "osteoclasts," effect their work is not known, but their presence where absorption of hard tissues is going on is universal. Some suppose that they put forth amœbiform processes, others that they secrete an acid fluid, but nothing very definite is known; a curious parallel is afforded by the manner in which a fungus can drill and tunnel through and through the dentine, as may be very constantly observed in teeth long buried.

The process of absorption once commenced does not necessarily proceed without intermission, but may give place for a time to actual deposition of osseous tissue on the very surface eroded; probably by the agency of the absorbent cells themselves, which are capable of being calcified in the excavations they have individually made.

These alternations of absorption and deposition, so common a result of inflammations of the pulp, or of the alveolo-dental periosteum, as to be diagnostic of the former occurrence of these maladies, often occur during the normal process of the removal of the deciduous teeth, and result in the deposition of a tissue not unlike cementum in excavations made in the dentine, or even in the enamel.

The eruption of the permanent teeth is a process closely analogous to that of the temporary set. Rapid absorption of the bone, especially on the exterior surface of the crypts, takes place, and an orifice very much larger than the crown of the tooth is quickly opened out.

Hence it is that the slightest force will suffice to determine the direction assumed by the rising crown: a fragment of a

root of a temporary tooth, the action of the lips and tongue, &c., are all potent agencies in modifying the arrangement of the teeth.

The temporary teeth stood vertically, the permanent teeth in front of the mouth stand obliquely, thus opening a space between the lateral incisors and the first bicuspid for the canine, which during development was out of the line altogether. And, inasmuch as the crowns of the teeth are on the whole much larger than their necks, it would be manifestly impossible for them all to come down simultaneously.

The permanent teeth usually make their appearance in the following order :—First permanent molars, about the seventh year ; a little later, the lower central incisors, upper centrals and laterals, the first bicuspids, the canines, the second bicuspids, the second permanent molars, the third permanent molars.

The period of eruption is variable. From a comparison of several tables, I find the principal discrepancies to relate to the date of the appearance of the canines and the second bicuspids. The canine would certainly appear to belong to the eleventh and twelfth years ; but some authors consider that the second bicuspid is usually cut earlier, others later than this date.

We may now revert to the phenomena observed in the alveolar processes. They were first built up as crypts with overhanging edges enclosing the temporary teeth : then they were swept away, in great part, to allow of the eruption of the temporary teeth ; and next they were rebuilt about their necks, to form their sockets.

Once more, at the fall of the deciduous teeth, the alveoli are swept away, the crypts of the permanent teeth are widely opened, and the permanent teeth come down through the gaping orifices.

When they have done so, the bone is reformed so as to

closely embrace their necks, and this at a period when but little of the root has been completed.

Take for example the first upper or lower molars: their short and widely open roots occupy the whole depth of the sockets, and reach respectively nearly to the floor of the antrum and the inferior dental canal. No growth, therefore, can possibly take place in these directions; the utmost available depth has already been reached, and as the roots lengthen the sockets must be deepened by additions to their free edges.

It is impossible to insist too strongly upon this fact, that the sockets grow up with and are moulded around the teeth as the latter elongate. Teeth do not come down and take possession of sockets more or less ready made and pre-existent, but the socket is subservient to the position of the tooth; wherever the tooth may chance to get to, there its socket will be built up round it.

Upon the proper appreciation of this fact depends our whole understanding of the mechanism of teething; the position of the teeth determines that of the sockets, and the form of the pre-existent alveolar bone has little or nothing to do with the disposition of the teeth.

During the period of eruption of the permanent teeth the level of the alveolar margin is seen, in a dried skull, to be extremely irregular, the edges of the sockets corresponding to the necks of the teeth, whether they have attained to their ultimate level, or have been but just cut.

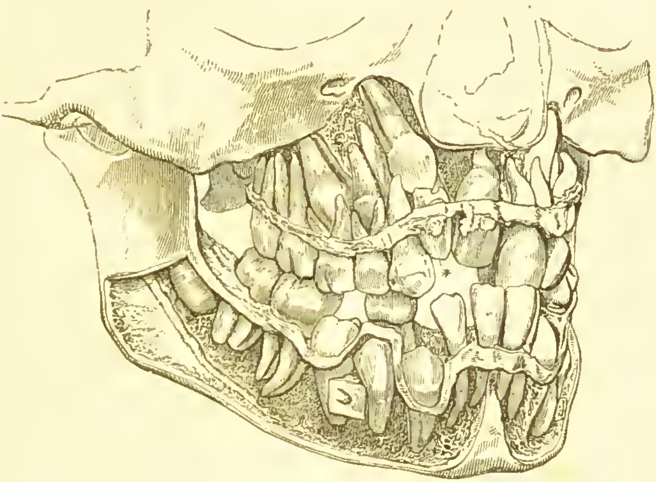
And when temporary teeth have been retained for a longer period than is natural, they sometimes become elevated to the general level of the permanent teeth (which is considerably higher than that of the temporary teeth), so that they take their share of work in mastication. When this is the case the alveoli are developed round them, and come to occupy with their tooth a higher level than before.

Enough has perhaps been said to illustrate the entire

dependence of the alveoli upon the teeth, a relation of which dentists every day avail themselves in the treatment of regulation cases: it remains to say a few words as to the forces which do determine the position of the teeth.

Inasmuch as when a tooth leaves its bony crypt, the bone

Fig. 88 (1).



does not at first closely embrace it, but its socket is much too large for it, a very small force is sufficient to deflect it. And, indeed, a very slight force, constantly operating, is sufficient to materially alter the position of a tooth, even when it has attained to its full length.

Along the outside of the alveolar arch the muscular lips are exercising a very symmetrical and even pressure upon the crowns of the teeth; so also the tongue, with equal symmetry, is pushing them outwards: between the two forces,

(1) From a child aged fourteen. The specimen well exemplifies the fact that the height of the alveolar edge corresponds exactly to the position of the neck of each tooth, on which it is wholly dependent. A temporary tooth (the first right lower temporary molar) has been elevated, so that it has attained to the level of the surrounding permanent teeth, and the edge of the socket follows the level of the neck of the tooth.

the lips and the tongue, the teeth naturally become moulded into a symmetrical arch. That the lips and tongue are the agencies which mainly model the arch is very well illustrated by that which happens in persons who have from childhood suffered from enlargement of the tonsils, or from adenoid growths in the pharynx, and are consequently obliged to breathe through an open mouth. This causes a slight increase in the tension of the lips at the corners of the mouth, and is impressed upon the alveolar arch as an inward bending of the bicuspids at that point; thus persons with enlarged tonsils will be found, almost invariably, to present one of the forms of mouth known as V-shaped.

But Dr. Norman Kingsley attaches far more importance to disturbed innervation than to any mechanical causes, and refers most dental irregularities to unhealthy conditions of the child's nervous system.

When the crowns of the teeth have attained such a level as to come in contact with their opposing teeth, they very speedily, from readily intelligible mechanical causes, are forced into a position of perfect correspondence and antagonism; and even at a somewhat later period than that of eruption, if this antagonism be interfered with, the teeth will often rise up so as to readjust themselves in this respect.

The roots of the central incisor teeth are completed at about the tenth year, the laterals a little later.

The canines are not quite complete at the twelfth year, but both first and second bicuspids are.

The first permanent molar is completed between the ninth and tenth year.

The second permanent molar between the sixteenth and seventeenth year.

The third between the eighteenth and twentieth.

These data are taken from a paper by Dr. Pierce (*Dental Cosmos*, 1884).

THE ATTACHMENT OF TEETH.

Although the various methods by which teeth are fixed in their position upon the bones which carry them pass by gradational forms into one another, so that a simple and at the same time absolutely correct classification is impossible, yet for the purposes of description four principal methods may be enumerated, namely, attachment by means of fibrous membrane, by a hinge, by anchylosis, and by implantation in bony sockets.

Attachment by means of Fibrous Membrane.—An excellent illustration of this manner of implantation is afforded by the Sharks and Rays, in which the teeth have no direct connection with the cartilaginous, more or less calcified, jaws, but are embedded solely in the tough fibrous mucous membrane which covers them. This, carrying with it the teeth, makes a sort of sliding progress over the curved surface of the jaw, so that the teeth once situated at the inner and lower border of the jaw, where fresh ones are constantly being developed, rotate over it, and come to occupy the topmost position (cf. description of the dentition of the sharks). That the whole fibrous gum, with the attached teeth, does really so slide over the surface of the jaw, was accidentally demonstrated by the result of an injury, which had been inflicted upon the jaws of a shark.

The fibrous bands by which each individual tooth of the shark is bound down are merely portions of that same sheet of mucous membrane which furnished the dentine papillæ; and the gradual assumption of the fibrillated structure by that portion of the mucous membrane which is contiguous to the base of the dentine papilla may be traced, no such fibrous tissue being found at the base of young papillæ, and very dense bands being attached to the bases of the completed calcified teeth.

A large number of fish have their teeth attached to short pedestals of bone by means of a sort of annular ligament, which allows of a slight degree of mobility.

By the limitation of this ligament to one side, where it is greatly strengthened, we pass by easy transitions to those more specialised arrangements characteristic of hinged teeth.

Attachment by an Elastic Hinge.—The possession of moveable teeth, able to yield to pressure and subsequently to resume the upright position, was formerly supposed to be confined to the Lophius (Angler) and its immediate allies. I have however found hinges in the common Pike (Esox), and in the Gadidæ (Cod tribe); so that, as they occur in these fish so widely removed from one another in other respects, it is probable that further investigation will bring, and indeed is bringing, to light many other examples of this very peculiar method of attachment, eminently suited to, and hitherto only discovered in, fish of predatory habits.

In the Angler, which obtains its food by lying in ambush on the bottom, to which it is closely assimilated in colour, many of the largest teeth are so hinged that they readily allow an object to pass into the mouth, but rebounding again, oppose its egress. These teeth are held in position by dense fibrous ligaments radiating from the posterior side of their bases on to the subjacent bone, while the fronts of the bases of the teeth are free, and, when the teeth are pressed towards the throat, rise away from the bone. The elasticity of the ligament is such that when it has been compressed by the tooth bending over towards it, the tooth returns it instantly into position with a snap. Many of the teeth of the Angler are, like most fishes' teeth, anchylosed firmly.

The Hake (Merlucius, one of the Gadidæ) possesses two rows of teeth, the inner and shorter of which are anchylosed, whilst the outer and longer are hinged.

In some respects these hinged teeth are more highly specialised than those of the Angler, which they resemble in being attached by an elastic hinge fixed to their inner sides,

FIG. 89 (1).

the elasticity of which is brought into play by its being compressed, or at all events bent over, upon itself.

The pulp is highly vascular, and its vessels are so arranged that, by entering the pulp through a hole in the ligament,

(1) Hinged tooth of Hake. *a.* Vaso dentine. *b.* Pulp. *c.* Elastic hinge. *d.* Buttress of bone to receive *f*, formed out of bone of attachment. *e.* Bone of jaw. *f.* Thickened base of tooth. *g.* Enamel tip.

which is about at the axis of motion, they escape being stretched or torn during the movements of the tooth. But the base of the tooth itself is modified so as to be particularly fitted for resisting the jars to which a moveable tooth must at times be exposed, and so is the bone upon which it is set.

As is seen in the figure, the base of the tooth, on the side opposite to the hinge, is thickened and rounded, the advantages which such a form must possess over a thin edge when bumping upon the bone being sufficiently obvious. This thickened edge is received upon a little buttress of bone, and it occupies a much higher level than the opposite thin edge to which the hinge is attached, so that the tooth cannot possibly be bent outwards without actual rupture of the ligament.

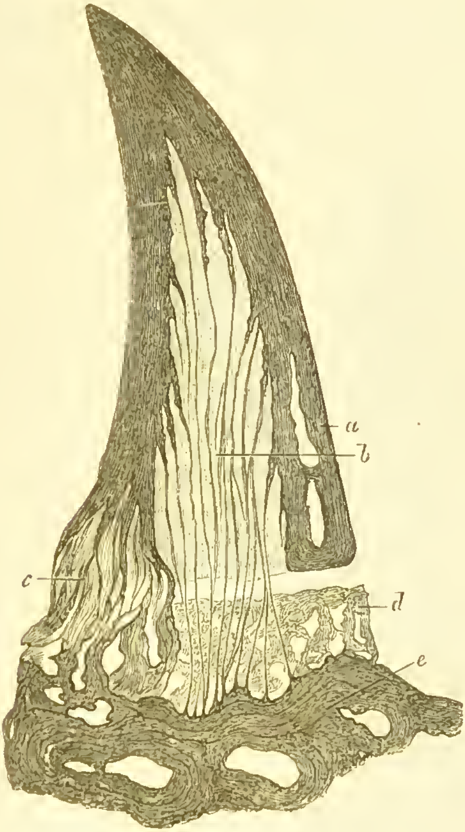
And what is not a little remarkable is, that whilst the Hake, the most predatory of all the Gadidæ, is possessed of these very perfectly hinged teeth, other members of the family have teeth moveable in a less degree, whilst others again have teeth rigidly fixed. So that within the limits of a single family we have several steps in a gradual progression towards a very highly specialised organ.

In the hinged teeth already alluded to the purpose served by their mobility seems to be the catching of active fish, and the elasticity resides solely in the hinges; but the common Pike possesses many hinged teeth which seem to be concerned in the swallowing of the prey after it has been caught, and there is no elasticity in the hinges, the resilience of the teeth being provided for in another way.

The teeth which surround the margins of the jaws are anchylosed, and they are more or less solidly filled up in their interior with a development of osteodentine, which, by becoming continuous with the subjacent bone, cements them upon it. The manner of development of this is by rods of calcifying material shooting down through the central pulp (see page 175); in the hinged teeth also these trabeculæ shoot

down, and become continuous with the subjacent bone, only instead of rigidly ossifying they remain soft and elastic, so

Fig. 90 (1).



that the tooth is like an extinguisher fastened down by a large number of elastic strings attached to different points on its interior, and hinged at one side.

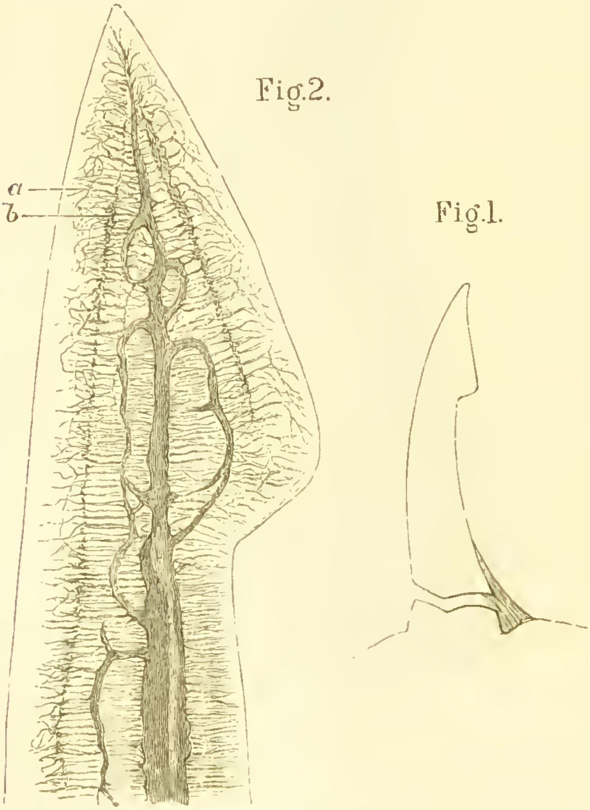
The elasticity is very perfect, so that the teeth depressed and suddenly released return with an audible snap, but it

(1) Hinged tooth of Pike. *a*. Dentine. *b*. Elastic rods, formed of uncalcified trabeculæ which might have become bone. *c*. Hinge, not itself elastic. *d*. Bone of attachment. *e*. Bone of body of jaw.

resides solely in these strings, for if these be divided by carefully slipping a cataract needle under the tooth without injuring the hinge, the tooth will stay in any position into which it is put.

Amongst the very peculiar predatory fish which were obtained by the Challenger from great depths, and which

FIG. 91 (1)



have been described by Dr. Günther, through whose kindness I have had the opportunity of examining them, are several which possess hinged teeth. Thus in Bathysaurus ferox, which

(1) Hinged tooth of Odontostomus. *a*. Enamel penetrated by dentinal tubes. *b*. Dentine.

has a crocodile-like snout, the teeth are of no very great size, but they are attached by ligamentous hinges which allow of their being bent down backwards and inwards. The teeth are not perched upon any definite pedestals, so that the motion is not very exactly limited to one plane. But in Odontostomus hyalinus there are some more highly specialised hinged teeth, which are laterally compressed, and have a sort of barbed point which recalls the form of some primitive bone fish-hooks. The vomer carries two such teeth of great length, behind which come some smaller ones: they are perched upon little bony pedestals of such form that the attachment being made by means of an elastic ligament on one side, the motion permitted to the tooth is strictly confined to one plane.

Thus we have examples of hinged teeth occurring in several distinct orders of fish; in Acanthopterygii (Lophius), in Anacanthina (Merlucius), in Physostomi (Esox, Bathysaurus, Odontostomus), whilst on the other hand they are not universal even within the limits of well-defined families.

The points most noteworthy are, (i.) that hinged teeth have arisen independently in families of fish widely removed from one another, and (ii.) that, whilst the general object of mobility and elastic resiliency is attained in all, it is by a different mechanism, and by the least possible modification of the existing fixed teeth of the family.

Attachment by Anchylosis.—In both the socketed and the membranous manners of attachment an organised, more or less vascular membrane, intervenes between the tooth and the jaw-bone; in the method now under consideration there is no such intervening membrane, but the calcified tooth substance and the bone are in actual continuity, so that it is often difficult to discern with the naked eye the line of junction.

The teeth may be only slightly held, so that they break off under the application of only a moderate degree of force, or they may be so intimately bound to the bone that a portion of the latter will usually be torn away with the tooth.

A very perfect example of attachment by anchylosis is afforded by the fixed teeth of the Pike, of which the central cone is composed of osteodentine. The method by which the entire fusion of this tissue with the bone beneath it takes place has already been alluded to, the similarity of its method of calcification with that of bone rendering the fusion easy and complete.

And in certain extinct fish, whose nearest ally is the now anomalous Australian shark, the Cestracion philippi, the lower part of the tooth is composed of osteodentine, which so closely resembles bone itself that it is impossible to say at which point the bone may be said to commence and the tooth to end; but even where this intimate resemblance in histological character does not exist, there is often to be found more or less blending of the basal dentine with the bone beneath it, so that there is even here a sort of transitional region.

From the accounts which pass current in most text books it would be supposed that the process of attachment by anchylosis is a very simple matter, the base of the dentine papilla, or the dental capsule, by its calcification cementing the tooth on to a surface of the jaw-bone already formed. In a few animals which I have examined(1), however, I have found that this conception does not at all adequately represent what really takes place; it seldom, perhaps never, happens that a tooth is attached directly to a plane surface of the jaw which has been formed previously; but the union takes place through the medium of a portion of bone (which may be large or small in amount) which is specially developed to give attachment to that one particular tooth, and after the fall of that tooth is itself removed.

For this bone I have proposed the name of "bone of attachment," and it is strictly analogous to the sockets of those teeth which have sockets. It is well exemplified in

(1) Transactions of the Odontological Society, Dec. 1874.—"Studies on the Attachment of Teeth."

the Ophidia, a description of the fixation of the teeth of which will serve to convey a good idea of its general character. If the base of one of the teeth, with the subjacent jaw-bone, be submitted to microscopic examination we shall find that the layer of bone which closely embraces the tooth contrasts markedly with the rest of the bone. The latter is fine in texture its lacunæ, with their very numerous fine

Fig. 92 (1).

canaliculi, very regular, and the lamination obviously referable to the general surface of the bone. But the "bone of attachment" is very coarse in texture, full of irregular spaces, very different from the regular lacunæ, and its lamination is roughly parallel with the base of the tooth. The dentine of the base of the tooth also bends inwards (Fig. 92), and its tubes are lost in the osseous tissue, a blending so intimate resulting, that in grinding down sections the tooth and the bone of attachment often come away together, the

(1) Section of tooth and a portion of the jaw of a Python, showing the marked difference in character between the bone of attachment and the rest of the bone.

tooth and this bone being more intimately united than this special bone is with that of the rest of the jaw.

A study of its development also proves that it has an intimate relation with the tooth with which it is continuous, for it is wholly removed with the fall of the tooth, and is specially developed again for the next tooth which comes into position. The periosteum of the rest of the jaw-bone appears to take an important share in the formation of this special bone substance, and the tooth capsule, by its ossification, apparently contributes little.

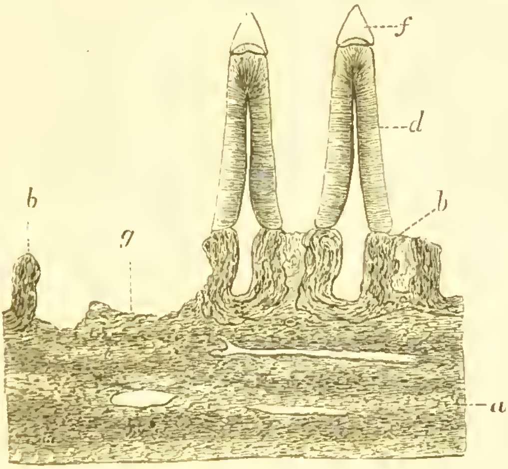
In the frog the teeth are commonly described as being attached by their bases and outer surface to a continuous groove, of which the external wall is the highest. Such is, however, an inadequate description of the process, the tooth as seen in section, being attached on its outer side by a new development of special bone, which extends for a short distance up over its external surface; and for the support of its inner wall there springs up from the subjacent bone a pillar of bone, which is entirely removed when that tooth falls, a new pillar being developed for the next tooth.

When the teeth are, as in many fish, implanted upon what to the naked eye appears nothing more than a plane surface of bone, a microscopic examination generally, in fact in all specimens which I have examined, reveals that the individual teeth are implanted in depressions much larger than themselves, the excess of space being occupied by new and specially formed bone, or else that the teeth surmount pedicles, which are closely set together, the interspaces being occupied with a less regular calcified structure.

A good example of the latter method is afforded by the Eel (Fig. 93), in which each tooth surmounts a short hollow cylinder of bone, the lamination, &c., of which differs strongly from that of the body of the jaw-bone. When the tooth which it carries is shed, the bone of attachment, in this case a hollow cylinder, is removed right down to the level of the main bone of the jaw, as is well seen in the figure to the left of

the teeth in position. Under a higher magnifying power the bone at this point would be found to be exeavated by "Howship's laeunæ." As an anehylosis, the implantation of the teeth is less perfeet than that of those of the snake, for the dentinal tubes at the base of the tooth are not defleeted, and do not in any sense blend with the bone beneath them. Aecordingly, the teeth are far less firmly attaehed, and break off quite readily.

FIG. 93 (1).



A transition towards the soeketed type of implantation is furnished by some of the eod family. In the haddoek, for example, the teeth surmount hollow cylinders of "bone of attaehment," resembling in many particulars those of the eel; the teeth do not, however, simply surmount the bony cylinders, but are eontinued for a short distanee within them, definite shoulders being formed whieh rest on the rims of the eylinder. The base of the tooth does not, however, eontraet or taper any more, and is widely open, so that it eannot be considered that any close approximation to a root is made.

(1) From lower jaw of an Eel. *a.* Bone of jaw. *b.* Bone of attachment. *d.* Dentine. *f.* Enamel. *g.* Space vacated by a shed tooth.

The pulp cavity of the tooth becomes continuous with the cavity of the osseous cylinder, into which it is for a short distance continued.

The bony supports of the teeth originate in many osseous trabeculæ which spring up simultaneously from the bone of the jaw beneath the new tooth ; these coalesce to form a net-like skeleton, which rapidly becomes filled in by the progress of ossification. So far as my own researches enable me to say, there is this much in common in all forms of

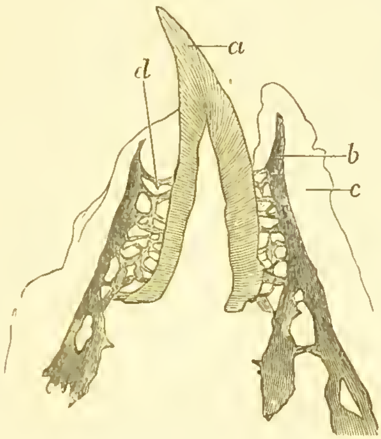
Fig. 94 [1].

attachment by anchylosis, no matter how different the naked eye results of the process may be ; the tooth, as it comes into position, is secured by an exceedingly rapid development of bone, which is more or less directly an outgrowth from the jaw-bone itself, which is in some unseen manner stimulated into activity by the proximity of the tooth. In amount this specially formed bone varies greatly, but in all instances it is not the tooth capsule, but tissues altogether external to this, which serve to secure the tooth in its place by their ossification.

[1] From lower jaw of a Haddock. *a.* Bone of jaw. *b.* Bone of attachment. *d.* Dentine of tooth.

The teeth of the mackerel present an interesting variety of attachment by anchylosis. The margins of the jaws are very thin, and by no means fleshy, and in this thin margin there is a deep groove between the outer and inner plate of the bone. In this groove are the teeth, their sharp points projecting beyond the edges of the bone, and they are held in their place by a network or scaffolding of bone of attachment which is developed between their sides and the inner

Fig. 95 (1).



surface of the bone. They are, so to speak, hung up in their place, and their open bases rest on nothing, or at least on nothing hard.

Attachment by implantation in a socket.—In this, as in anchylosis, there is a special development of bone, which is modelled to the base of the tooth, but instead of its being in actual close continuity with the dental tissues, there intervenes a vascular organised membrane. The manner in which the sockets are, so to speak, plastered

(1) Tooth of Mackerel, showing its peculiar mode of anchylosis. *a.* Tooth. *b.* Bone of jaw. *c.* gums and stems. *d.* Bone of attachment.

around the roots of the teeth, and are perfectly subservient to and dependent on them, has already been described ; little, therefore, need be added here, save that the soft tissue intervening between the bone and the tooth is not separable, either anatomically or from the point of view of development, into any two layers, but is a single membrane, termed the "alveolo-dental periosteum." That it is single, is a matter of absolute certainty; there is no difficulty in demonstrating it *in situ*, with vessels and bundles of fibres traversing its whole thickness from the tooth to the bone, or *vice versâ*.

The nature and development of the sockets in those few reptiles and fishes which have socketed teeth require further examination. I am not, from what I have seen in sections of the jaws of a young crocodile, inclined to regard them as in all respects similar to the alveoli of mammalian teeth. At all events they are not developed in that same subserviency to each individual tooth ; on the contrary, successive teeth come up and occupy a socket which is more or less already in existence.

Although there are animals in which implantation in a spurious socket is supplemented by anchylosis to the wall or to the bottom of the socket, no example of anchylosis occurring between the tooth and the bone of the socket has ever been met with in man, or indeed in any mammal exemplifying a typical socketed implantation of the teeth.

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Tomes, J. Dental Surgery. 1859.
Humphery. Transact. Camb. Philos. Soc. 1863.
Wedl. Pathology of the Teeth.
Heudner. Beitrage zur Lehre von der Knochenentwickelung, &c.
Tomes, Charles S. On Vascular Dentine and Hinged Teeth. Philos. Transac., 1878. and Quart. Journal Micros. Science, vol. xvii. new series.
Transac. Odontolog. Soc. 1874—1876.

CHAPTER VI.

THE TEETH OF FISHES.

In the following pages nothing more than a brief account of a few typical forms can be attempted; the limits of space forbid the mention of many creatures, or the insertion of detailed descriptions of the dentition even of the few which are included. In the class of fish the task of selection of the forms for description is no easy one; for the almost infinite diversity of dentition which exists in it makes it a matter of peculiar difficulty to frame any general account, or to do more than present before the reader a description of a few individual forms from which he may gather, as best he can, a general idea of piscine dentition.

The class of Fishes is divided into four sub-classes:—

Leptocardii. Heart replaced by pulsating sinuses. Skeleton notochordal and membrano-cartilaginous. No skull, no brain.

Cyclostomata. Head without bulbus arteriosus. Skeleton cartilaginous and notochordal. No jaws; mouth surrounded by a circular lip.

Teleostei. Non-contractile bulbus arteriosus. No spiral valve in intestine. Optic nerves decussating. Skeleton ossified, with completely separated vertebræ.

Palæichthyes. Heart with contractile conus arteriosus; intestine with spiral valve; optic nerve non-decussating or only partially decussating.

Of Leptocardii (the single genus Amphioxus or Branchiostoma), there is nothing to be said, as it has no jaws and therefore no teeth.

The Cyclostomata comprise the lampreys and the very peculiar parasitic fishes, the Myxine and Bdellostoma, which

bore their way into the bodies of other fish ; the cod is often attacked by the Myxine. The lampreys, which also are predatory, attaching themselves by their sucking mouth to the bodies of other fish from which they scrape off the flesh, have a round mouth, the margins of which are beset with rows of small conical teeth, there being two larger blade-shaped teeth, called from their relative position the mandibular and maxillary teeth in the centre.

Until recently little was known of the structure of horny teeth, but they have been investigated by Dr. Beard (Centralblatt f. Wissen. Anat. iii. 1888, nr. 6), who finds that the horny cone rests upon a slight dermal papilla, and fits into special epidermal depressions at the base of the papilla (in Pteromyzon fluviatilis) ; but in P. marinus there are three superimposed cones, "like a nest of Chinese boxes." Each of these layers arises from a separate epidermal depression, which goes on continually forming horn, so that the under cones are in no sense reserve teeth, for as each tooth is worn away at the apex fresh horny matter is formed below and pushed forwards. There is thus no resemblance to the teeth of higher vertebrates.

In a young lamprey there are to be found what at first sight look like true tooth sacs, but the dental papilla never forms any odontoblasts, and the epithelium which corresponds to the enamel organ produces horn ; this is true of the marginal teeth, but further in towards the centre the teeth are formed simply in the basal layers of the epithelium, without the intervention of any sort of tooth sac.

But in the Myxine and Bdellostoma there is a very interesting and unexpected arrangement of structures. They have a large sharply pointed median tooth and two comb-like smaller teeth upon the tongue, and the working surface of the teeth is composed of horn similar both in structure and development to that found in the lamprey.

Dr. Beard describes the tooth of Bdellostoma as consisting

of a cap of horn which is thick and strong and of a bright yellow colour; beneath this comes a layer of epithelium, and next to this a hard calcified material, which is to be regarded as some form of dentine.

The horny cap is fitted into an epithelial groove at its base, so that it increases in length from the cells of this groove becoming cornified, and in thickness by a similar conversion of the epithelial layer beneath it.

The hard cone which forms, so to speak, the body of the tooth is an anomalous structure not closely corresponding with any known form of dentine, but yet it is undoubtedly the product of an odontoblast layer upon the pulp, which latter remains in the base of the cone of dentine in the usual way.

The great hardness of the tooth and of the horny cap renders it a very difficult matter to get good sections, and hence the minute structure has not been very fully described. At the apex of the cone is a thin structureless layer, which Dr. Beard thinks may be enamel (the frequent occurrence of thin outer structureless layers upon dentine however would seem to render this determination open to uncertainty). There is, however, a layer of epithelium, in the proper situation, which has the characters of an enamel organ in so far as the presence of long columnar cells go.

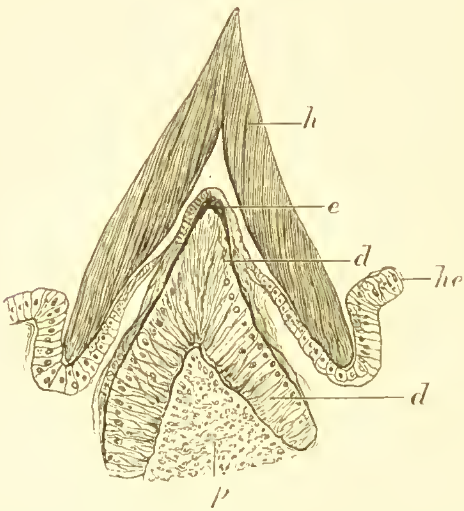
The dentine cap appears to contain small dentinal tubes, and also vascular canals of larger size arranged with considerable regularity.

It is difficult to conceive that the presence of the calcified cone can be of much, if any, service whilst buried beneath the horny cap, and we must regard these horny teeth not as an earlier and simple form of tooth, but as being degenerated teeth. And they would thus lend support to the idea already arrived at on other grounds that these fish had as ancestors fish which had jaws and teeth carried upon them.

It is to be noted that the relation which the horn cone bears to the dental papilla and to its dentine is entirely different from that borne by the horny teeth of Ornithorhyncus, in which the horny plate which takes the place of teeth in the adult lies beneath the teeth.

It has been suggested by Dr. Beard that the fusion of the

FIG. 96 (1).



lingual teeth of Myxine into a serrated plate may indicate the manner in which the serrated horny jaws of Chelonians may have originated, as a substitution of horny tissue for true teeth upon which they were once superimposed; and similar speculations have been indulged in as to the manner in which the bird's bill may have originated from the substitution of a number of coalescent horny teeth for true teeth, but the material for such generalisation is not yet to hand.

As in the matter of teeth the Palæichthyes, comprising the Sharks and Rays and the Ganoid fish, present somewhat simpler

(1) Tooth of Bdellostoma, Semidiagrammatic, after Dr. Beard. *d.* Calcified dentine cap. *e.* (?) Enamel. *h.* Horny tooth. *he.* Epithelial groove in which the bone is formed. *p.* Pulp.

conditions that are met with in the osseous fish, it will be convenient to describe their teeth first, although in most respects they stand at the head of the class of fishes, and present many indications of affinity with the Batrachia.

In Sharks the scales are replaced by calcified papillæ, which have the structure of the teeth: to these the "shagreen," as shark skin is termed, owes its roughness; the mouth is a transverse, more or less curved fissure, opening upon the under surface of the head at some little distance behind the end of the snout. Hence it is that a shark in seizing its prey turns over upon its back or at all events upon its side.

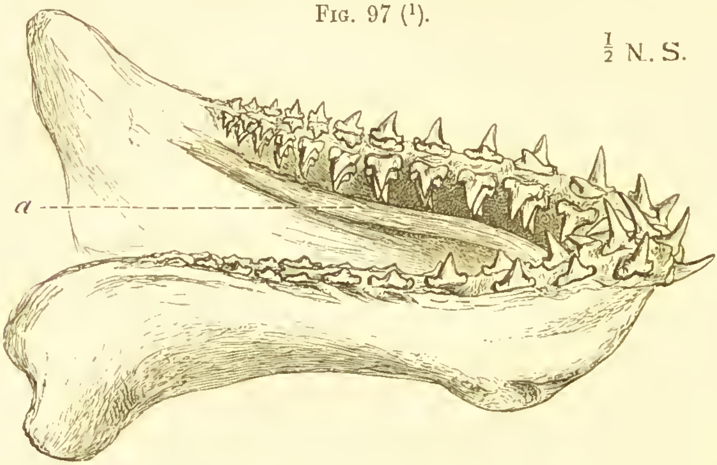
The jaws, which are made up of the representatives of the palato-quadrate arch, and of Meckel's cartilage, neither true maxillæ nor premaxillæ being present, are cartilaginous in the main (although covered with a more or less ossified crust), and therefore shrink and become much distorted in drying. The shape of the jaws differs in the various groups of Plagiostomi, in some each of the two jaws being a tolerably perfect semicircle, while in others they are nearly straight and parallel to one another (see Fig. 97 and Fig. 101); but in all the rounded working surface of the jaw is clothed or encased by teeth, which are arranged in many parallel concentric rows.

The teeth, which are situated upon the edge or exposed border of the jaw, are usually erect, whilst the rows which lie behind them, farther within the mouth, point backwards, and are more or less recumbent, not having yet come into full use.

In this respect, however, marked difference exists among various genera of sharks; for instance in the great tropical white shark the teeth which lie on the border of the jaw are erect, and all the successive rows are quite recumbent, whereas in many of the dog-fishes the inner surface of the jaws forms an even rounded surface along which the rows of

teeth are disposed in every intermediate position between those fully recumbent at the innermost part of the jaw, and those fully erected upon its exposed borders. Only a few of the most forward rows of teeth are exposed, a fold or flap of mucous membrane covering in those teeth which

FIG. 97 (1).



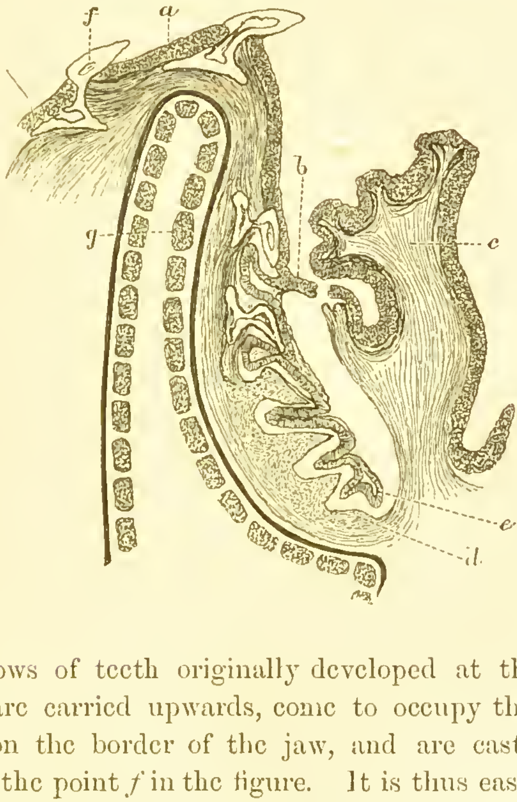
are not as yet fully calcified and firmly attached to the gums.

In Lamna, which may be taken as fairly illustrative, the teeth are arranged round the jaws in concentric rows with great regularity, the teeth of the successive rows corresponding in position to the teeth of older rows, and not, as is the case in some other sharks, to their interspaces. They are attached by being embedded in a densely fibrous gum, which closely embraces their bifurcated bases; and this dense gum, carrying with it the teeth, slides bodily upwards over the inner face of the jaw, and outwards over its border, beyond which it, to borrow a phrase from geological science, has an "outcrop."

(1) Lower jaw of Lamna. *a*. Edge of flap of mucous membrane which covers in the teeth not yet completed.

In Lamna the second and third rows of teeth are only partially erect, the rows behind these lying recumbent, and being in the fresh state covered in by the fold of mucous membrane, which, being dried and shrunk in the specimen figured, falls short of its original level.

FIG. 98 (1).



Thus rows of teeth originally developed at the base of the jaw are carried upwards, come to occupy the foremost position on the border of the jaw, and are cast off when they pass the point *f* in the figure. It is thus easy to understand why sharks' teeth are so abundantly found in a fossil condition, although other indications of the existence of the

(1) Transverse section of lower jaw of a Dog-fish. *a*. Oral epithelium. *b*. Oral epithelium passing on to flap. *c*. Protecting flap of mucous membrane (thecal fold). *d*. Youngest dentine pulp. *e*. Youngest enamel organ. *f*. Tooth about to be shed. *g*. Calcified crust of jaw.

fish are rare enough; for every shark in the course of its life casts off great numbers of teeth, which fall to the bottom of the sea and become bedded in the deposit there forming.

The teeth are never anchylosed to the jaw, nor have they any direct connection with it, but, as before mentioned, are retained by being bedded in a very tough fibrous membrane; the nature of their fixation has been more exactly described at another page (page 213).

The sheet of fibrous gum slides bodily over the curved surface of the jaw, continually bringing up from below fresh rows of teeth, as was proved by André's specimen, and it may be worth while to condense from Professor Owen the description of the manner in which it was thus proved that an actual sliding or rotation of the membrane does really take place, and that the whole bony jaw itself does not become slowly everted. The spine of a sting ray had been driven through the lower jaw of a shark (Galeus), passing between two (vertical) rows of teeth which had not yet been brought into use; when the specimen came under observation the spine had remained in this situation, transfixing the jaw, for a long time, as was evidenced by all the teeth of these two rows, both above and below it, being stunted and smaller than their neighbours.

Hence the development of these teeth, which ultimately came to be at some little distance from the spine, had been profoundly modified by its presence, and it is difficult to understand in what manner this could have affected them had they not, at an earlier period of their growth, lain in more immediate proximity to it. But if the membrane, with the teeth attached, does move slowly along the surface of the jaw, this difficulty at once disappears.

The forms of the teeth in various sharks are different and characteristic; nevertheless they vary somewhat with age in some species, and present differences in size and

form in the upper and lower jaws, or in different parts of the mouth of the same individual. For instance, in Lamna, in the upper jaw, the third teeth of each horizontal row, counting from the middle line, are very small, while in both jaws there is a gradual diminution in the size of the teeth towards the back of the mouth.

Thus, although it is often possible to refer a particular tooth to its right genus or even species, much care is requisite in so doing.

The teeth of the bloodthirsty white shark (Carcharias) are triangular flattened plates, rounded on their posterior aspect, with trenchant slightly serrated edges; it is pointed out by Professor Owen that if the relation between the size of the teeth and that of the body were the same in extinct as in recent sharks, the dimensions of the teeth of the tertiary Carcharodon would indicate the existence of sharks as large as whales.

The intimate relationship between the teeth and the dermal spines, which from the standpoint of development, has been illustrated at page 2 and page 123, is apparent also in their histological structure. There are many dermal spines to be met with in the sharks, which seen alone could not possibly be distinguished from teeth, the resemblance both in outer form, in minute structure, and manner of development being most complete. The tooth figured on page 49 is a fair example of a structure very common among the sharks, viz., a central body of osteodentine, the outer portion of which has dentinal tubes so fine, regular, and closely packed as to merit the name of hard unvascular dentine, and over this again a thin varnish of enamel. (?)

And yet no observer from its structure alone could feel sure whether it was a large dermal spine, or a tooth. Dental tissues occur in other parts of the mouths of Selachia than upon the jaws, not only in the embryonic stages, but in the adult. Thus Professor Sir W. Turner has described (Proc.

Roy. Society, Edinburgh, 1880), very numerous comb-like appendages 5 inches long upon the branchial arches of the Basking Shark (Selache maxima), which apparently perform the same function as whalebone in straining the water. These combs are formed of a variety of dentine (? osteodentine), and closely resemble in structure the true teeth, which are however very small in this shark.

In the seas of Australia there exists a Shark, the Cestracion Philippi, with a very aberrant dentition, to which great interest attaches, inasmuch as it is the sole surviving representative of forms once spread all over the world. In the front of the mouth the teeth are small and very numerous; they are flat plates fitted by their edges to one another, while from their centres spring up sharp points, soon worn off when the tooth reaches such a position upon the jaw that it comes into use.

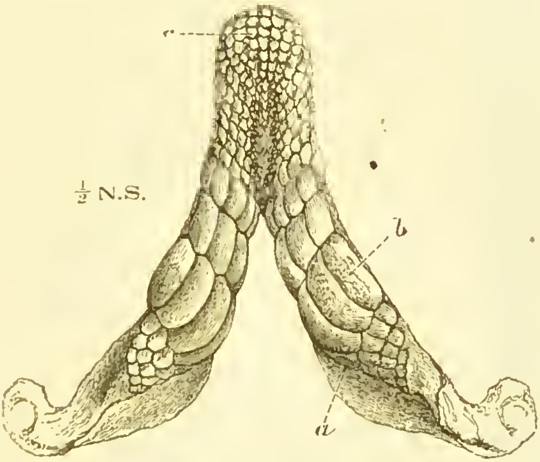
Proceeding backwards, the teeth cease to be pointed, increase in size, and become fewer in each row; a reference to the figure will convey a better idea of their general form than any description. Those which have come into use are, towards the back of the mouth, always much worn; their shedding and renewal takes place, as in other sharks, by a rotation of the mucous membrane over the surface of the jaw, so that, as might have been expected, large numbers of the isolated fossil teeth of Cestracionts are to be met with.

The teeth of the Cestracion are fitted for the trituration of hard substances, and for such they are used, its food consisting of shell-fish, &c. The teeth consist of vaso- and osteodentine, protected by what is apparently a structureless layer of enamel.

The extinct Cestracionts extended far back in time, being met with in palæozoic strata, and they were equally widely distributed in space; the size of many of the teeth also indicates the existence of forms much larger than the recent

timid and inoffensive Cestracion Philippi. Many of the extinct forms are known only by isolated teeth; of others portions of the jaw with teeth *in situ* have been discovered thus fragments of the jaw of Acrodus, the isolated fossil teeth of which have been compared to fossil leeches, with seven teeth arranged in series, have been met with.

FIG. 99 (1).



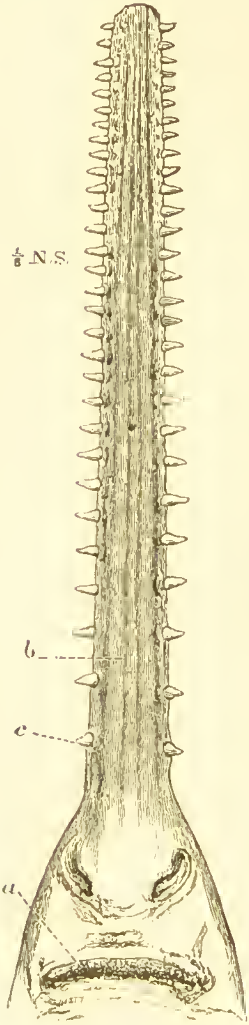
The Pristis, or Saw fish, so far as the mouth is concerned, is in no way remarkable, its teeth being small and blunt, like those of many rays. The snout is, however, prolonged to an enormous length, and is shaped like a gigantic spatula, its thin edges being beset by dermal spines of large size, arranged at regular intervals, and implanted in distinct sockets. These dermal spines, or rostral teeth, as they are sometimes termed, are not shed and replaced, but grow from persistent pulps; in structure they closely

(1) Lower jaw of Cestracion Philippi. *a.* Young teeth not yet in use. *b.* Large grinding back teeth. *c.* Small pointed front teeth.

The new teeth are developed at the bottom of the series on the inner side, and, just as in other sharks, are covered in by a flap of mucous membrane.

resemble the teeth of Myliobates (see page 88), being made up of parallel denticles, in the centre of each of which is a pulp cavity or medullary canal.

Fig. 100 ([1]).



What use the Saw-fish makes of its armed snout is not very certainly known, but its rostral teeth are of interest to the odontologist for several reasons—the one that they are dermal spines, having a structure all but identical with that of the actual teeth of another ray, the Myliobates; the other that they are socketed, a manner of implantation not at all common amongst the teeth of fishes; and yet another, that they grow from persistent pulps, also unusual in fishes.

Broadly speaking, the teeth of the Rays (skates) differ from those of typical sharks by being individually blunter, and being more closely set so that they form something approaching to a continuous pavement over the jaws, with but little interspace left between the teeth.

The dentigerous surface of the jaw is very much rounded, and in some is completely encased under a pavement of teeth. Thus, in Myliobates, the powerful jaws are straight from side to side, while their working surfaces

([1]) Rostrum and under side of the head of a small Pristis. *a*. Mouth. *b*. Rostrum. *c*. One of the rostral teeth.

The teeth, with which the margins of the jaws are covered, are so small that they cannot be represented in this figure.

from baek to front are segments of a eirele. The teeth form a thiek and strong pavement over the jaws, in the manner of their formation and renewal eonforming with the teeth of other Plagiostomi; the severe use to whieh they are put being indieated by the extent to whieh the grinding surfaees of those teeth which have eome into use are worn down.

Fig. 101 (1).

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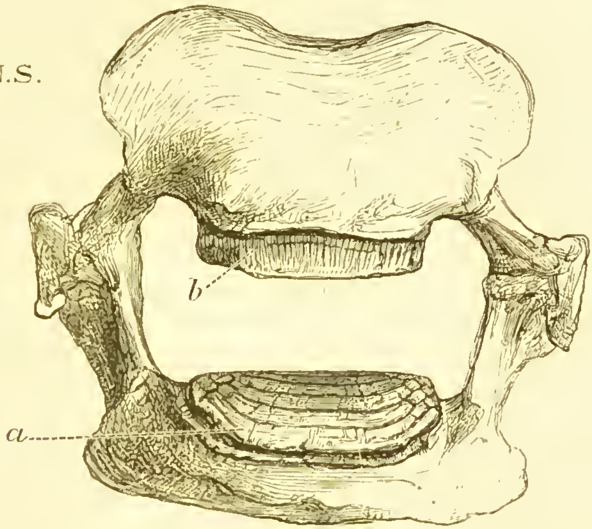


Several genera have the jaws thus covered, the number of the teeth differing; thus Myliobates has a central series of very broad, oblong teeth, to the outer sides of which are three rows of small hexagonal teeth; in Œtobatis the large oblong eentral plates eonstitute the whole armature of the jaw.

The strueture of the teeth of Myliobates has already been deseribed and figured (see page 88).

(1) Upper and lower jaw of Myliobates. At *a*, the mosaic pavement formed by the broad flattened plates which constitute its teeth is seen, these being the oldest teeth which are about to be shed off in consequence of the rotation of the whole sheet of mucous membrane over the surface of the jaws. The letter *b* indicates the under surface of one of the plates, which is seen to be finely fluted on its edge.

Near the borderland between fish and amphibia is the Lepidosiren, or Mud-fish, which is a fish rather than an amphibian. The armature of its mouth is peculiar, the margins of the lower jaws being formed by dental plates anchylosed to the bone. These plates have upon their edges five deep angular notches, the prominence of the upper plate corresponding to the notches of the lower; and the edge is kept somewhat sharp by the front surface being formed of very dense hard dentine, while the bulk of the tooth is permeated by large medullary canals, which render it softer. The cutting plates of the upper jaw are developed in the median line of the palate, and there are in front of them conical piercing teeth upon that forward prolongation of the cartilage which takes the place of a distinct vomer; these have sometimes been described as being upon the nasal bone.

It would seem that the two conical piercing teeth serve as holdfasts, while the cutting edges of the deeply-notched plates are brought into play to slice up the food.

Both in structure and general disposition the dental plates in Lepidosiren are paralleled by the teeth of Ceratodus, for some time known only as a fossil, but of which recent examples have been captured near Queensland; this resemblance was suspected some years ago by my friend, Prof. Moseley, of the *Challenger*, and has been since worked out by other observers.

Amongst ganoid fish great diversity of dentition exists. Thus the sturgeons have no teeth, the mouth being at the lower surface of the snout, and being protrusible as a sort of suctorial tube. In the larval stages, however, the sturgeon possessed teeth. In the allied Spatularia there are numerous very minute teeth, whilst there are numerous extinct ganoids with large blunt pointed teeth upon the palate and mandible.

Lepidosteus, the structure of whose teeth has been

described on p. 84, has a long pointed snout furnished with large sharp conical teeth.

The Teleostei, or osseous fish, form the group which comprises all the fish most familiarly known to us, and within its limits the variation in dentitions is so great that few, if any, general statements can be made about them. It is not uncommon to find teeth crowded upon every one of the bones which form a part of the bony framework of the mouth and pharynx, and the teeth are sometimes in countless numbers. And such is the variability that even within the limits of single families great differences in the teeth are to be found.

The teeth of fish are of all degrees of size and of fineness; in some (Chætodonts) the teeth are as fine as hairs, and are so soft as to be flexible; they are said to be horny.

Teeth which are very fine and very closely set are termed "dents en velours," "ciliiform" or "setiform;" when they are a little stouter, "dents en brosse," or "villiform;" and when still stronger and sharper, "dents en cardes." Teeth that are conical, wedge-shaped, spheroidal, and lamelliform, are all to be met with; in fact there is infinite diversity in the form of fishes' teeth.

And there are some fish, *e.g.*, some of the large Siluroid fishes, which have very strong, large teeth, an inch and a half or more long, and very firmly anchylosed to the bone.

The long and very strong snout of the Sword Fish, formed by a coalescence of maxillary and inter-maxillary bones, which is able to pierce a plank, is roughened on its lower surface by villiform teeth which can be of no use, and are therefore to be regarded as rudimentary survivals.

In the common pike the mouth is crowded with sharply-pointed teeth, having a general inclination backwards, and being in some parts of the mouth of larger size than in others. The margin of the lower jaw is armed with teeth of formidable size and sharpness, the smallest teeth being at the front, where they are arranged in several rows, and the

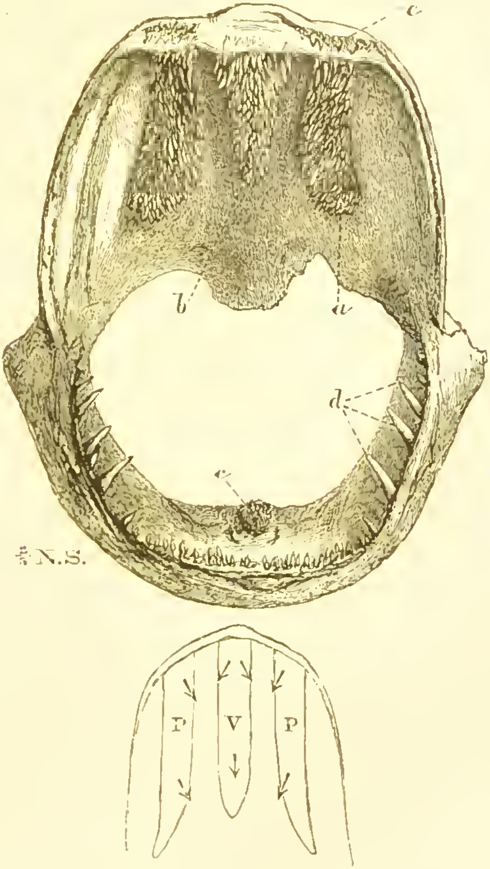
largest being about the middle of the side of the jaw. A pike, as is well known to anglers, when it has seized a fish often holds it across its mouth, piercing and retaining it by means of these largest teeth; then, after holding it thus for a time, and so having maimed it and lessened its power of escape, it swallows it, generally head foremost. The tenacity of the pike's hold is often illustrated when it takes a bait, and retains it so firmly that when the angler "strikes" the hooks do not get driven into the fish's mouth; but after tugging at the bait for a time the pike releases it, and the angler finds that it has never been hooked at all.

The margin of the upper jaw is not bordered by teeth, save at the front, where the intermaxillary bones carry a few teeth of insignificant dimensions; indeed, it is rather exceptional for the true maxillary bones to carry teeth in osseous fish. The roof of the mouth presents three wide parallel bands of teeth, those in the median band (on the vomer) being directed backwards, those upon the lateral bands (on the palatine bones) backwards and inwards. Some of the latter teeth are very large, but not quite so large as those at the sides of the lower jaw.

The marginal teeth are firmly anchylosed, but the teeth upon the palate are all hinged, and in such a manner that they can only bend exactly in one direction. Those of the vomerine band which lie in the middle line, will bend backwards only; those upon the outer margins of this band backwards, with an inclination outwards. Those of the lateral or palatine bands bend obliquely backwards and inwards, about at an angle of 45 with the median line of the mouth, or somewhat more directly backwards. To a body sliding over them in one direction they offer no resistance, bending down as it passes, and springing up as the pressure is removed from them, but to anything moving in any other direction they are rigidly fixed sharp curved stakes impeding its further progress.

An elongated body of some size, such as a living fish, can only be swallowed by the pike when it is arranged

Fig. 102 (1).



lengthwise in the mouth; crosswise it cannot possibly enter

(1) Jaws of a Pike, viewed from the front, with the mouth opened more widely than is natural, so as to bring the teeth into view. *a.* Group of teeth situated on the palatine bone. *b.* Group of teeth situated on the vomer. *c.* Group of teeth situated on the lingual bone. *d.* Specially large teeth, placed at intervals round the margin of the lower jaw. *e.* Group of teeth on the intermaxillary bones.

The diagram beneath represents the direction in which the hinged teeth of the vomerine and palatine bands can bend.

the throat. The hinged teeth on the palate seem admirably arranged for getting the fish into a longitudinal position and keeping it there; for, if we imagine the fish's body held up against these teeth, and consider the direction in which the hinging of the teeth allows them to yield, it will be seen that every motion tending to arrange the body lengthwise, either in the median line of the mouth or in either of the interspaces between the vomerine and palatine bands of teeth, will meet with no obstruction, but in every deviation from this position it will be caught on the points of the teeth and resisted. Thus with the pike's mouth shut, and the fish kept up against the palatine teeth, even its own struggles will be utilised by every movement tending to place it aright being allowed, and every other stopped by the bands of hinged teeth entangling it. The structure of these teeth, and the mechanism by which they are rendered elastic, have been already described (page 217).

The lingual bone, and the three median bones behind it, carry small teeth arranged in oblong patches; the internal surfaces of the branchial bones (which support the gills) are armed with similar small teeth; while the last or fifth branchial arch (which carries no gills, the bones forming it being called inferior pharyngeal bones,) carry larger teeth. The superior pharyngeal bones (which are median portions of the four anterior branchial arches) also carry recurved teeth larger than those which line the rest of the internal surfaces of each of the branchial arches.

The pike's mouth and pharynx thus fairly bristle with teeth, all directed somewhat backwards; and any one who has been unfortunate enough to have allowed his fingers to get entangled in the mouth of a living pike will realise how small a chance of its living prey has of escape, when once it has been seized.

The teeth of the pike are composed of a central body of osteo-dentine, on the outside of which is a layer in which

the dentinal tubes are directed towards the surface, as in hard or unvascular dentine (see fig. 48); while the outermost portion of all is a very dense and hard, and apparently structureless, enamel film. The teeth are anchylosed to the bone, and are very frequently renewed, their successors being developed at one side of their bases.

Though the pike has rather more teeth than many other fish, it may be taken as a fair example of most osseous fishes in this respect. Space will only allow of a few of the more exceptional forms being here described.

The angler (Lophius piscatorius), another predatory fish, with an enormous mouth and disproportionately small body and tail, lies hidden in the mud, or crouched upon the bottom, and makes a rush upon smaller fishes which approach sufficiently near to it; it is remarkable for the manner of attachment of the teeth, some of the largest of which upon the edges of its jaws do not become anchylosed, but are so attached, as has been described at p. 214, as to allow of their bending in and towards the mouth, but not in the opposite or any other direction. The teeth of the outer row are firmly anchylosed to the margins of the jaw, and the far larger hinged teeth form a sort of irregular second row.

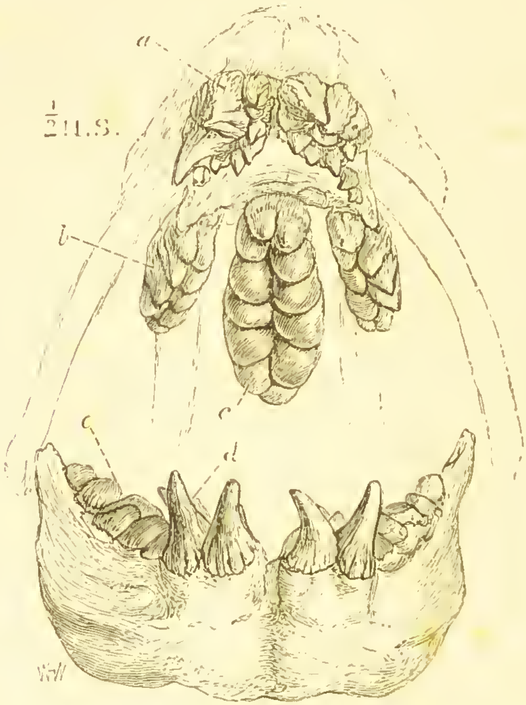
The benefit of such an arrangement to a fish of its habit is sufficiently obvious; its teeth allow the utmost freedom of entry, but offer obstacles to anything getting out again.

This arrangement of teeth, long supposed to be unique, is closely paralleled in a very different fish, the Hake (Merlucius, one of the Gadidæ). This fish, the most active and predatory of the Cod family, follows shoals of pilchards and of herrings, themselves active fish, and feeds upon them. The margins of the jaws carry two distinct and regularly arranged rows of teeth, an outer smaller row which are anchylosed, and an inner longer row which are hinged. They are very sharp, being tipped with spear points of enamel, and are recurved. In the fresh state they look

quite red, being composed of a richly vascular vaso-dentine.

Again, in several of the deep sea fish dredged by the

Fig. 103 (1).



Challenger from the depths to which light does not penetrate, hinged teeth have been found (cf. p. 218). Many of these deep sea fish have very formidable dental armaments, and curiously enough, one of these, which has exceptionally long upper teeth, has a downward projection from the lower

(1) Bones of the mouth of the Wolf-fish (Anarrhicas lupus). The letter *a.* indicates the divergent pointed teeth which occupy the intermaxillary bone ; the letter *d.* indicates the similar teeth which are attached to the front of the mandible, on the middle and back parts of which are round-topped crushing teeth (*c*). Strong crushing teeth are found also upon the palatine bones (*b*), and upon the vomer (*c*).

jaw, which serves to protect them while closed, an arrangement elsewhere only met with in extinct mammalia, such as Dinoceras and Machairodus figured later on in this work.

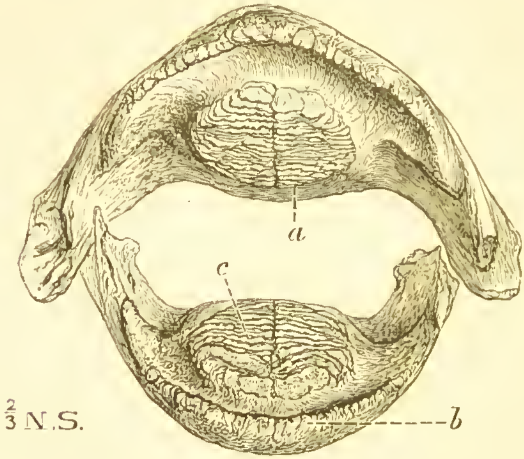
Another curious dentition is possessed by the Wolf-fish (Anarrhicas lupus), also an inhabitant of British waters, and sometimes to be seen in London fishmongers' shops under the name of the sea cat. The intermaxillary teeth are conical, bluntly pointed, and set forwards and outwards; these are antagonised by somewhat similar teeth in the front of the lower jaw. The palatine bones carry short, bluntly conical, or round topped crushing teeth in a double row; the vomer is also armed with a double row of very much larger and shorter teeth; the lower jaw, with the exception of its anterior part, is occupied by teeth of similar character.

All the teeth of the Wolf-fish are anchylosed slightly to the bone, a definite process from which forms a sort of short pedestal for each tooth. The jaws are worked by muscles of great power, and it seldom happens that a specimen is examined in which some of the teeth are not broken. It feeds upon shell fish, the hard coverings of which are crushed by the blunter teeth, while the pointed front teeth apparently serve to tear the shell fish from the rocks to which they are commonly attached.

In the group of fish known as "Gymnodonts" (naked toothed), the teeth and the margins of the dentigerous bones form a sort of beak, which is not covered by the lips. The example here figured consists of the upper and lower jaws of the Diodon, so called because it appears to casual observators to have but two teeth. A kindred fish in which the division of each jaw in the middle line is conspicuous, is similarly called Tetrodon. The jaw consists of teeth and bone very intimately fused together; the broad rounded mass (*c.* in the figure), which lies just inside the margin of the jaw, is made up of a number of horizontal plates of dentine, the

edges of which crop out upon its posterior surface; and these are united to one another by the calcification of the last remains of the pulp of each plate into a sort of osteo-

Fig. 104 (1).



dentine, the different hardness of the two tissues keeping the surface constantly rough, as the plates become worn away. The whole margin of the jaw is similarly built up of smaller horizontally disposed denticles, or plates of dentine, which are, as they wear down, replaced by the development of fresh plates, which are added from beneath, where they are developed in cavities situated low down in the substance of the bone.

The new teeth or plates of dentine thus formed at the base of the hemispherical masses within the jaws (at the point *a*), or low down in the substance of the jaw, do not come into use by the ordinary process of displacing their predecessors, and being in turn themselves replaced, but

(1) Jaws of the Diodon. *a.* Base of the dental plates, where new lamellæ of dentine are being developed. *b.* Margin of jaw, formed mainly by the sides of the denticles. *c.* Compound tooth, made up of the superimposed lamellæ of dentine anchylosed together.

fresh plates only come into use by the actual wearing away of all that is above them, both dentine and bone, so that they come to be the topmost portion of the jaw. The margins of the jaw are, however, mainly built up of dental tissues, there being but little bone in their interspaces.

Tetrodon has not the rounded triturating disk of the Diodon, or has it but feebly represented; and the margins of the jaws are sharper.

In the parrot-fishes (Scarus), which are not very nearly allied to the Gymnodonts, somewhat similar beaks are found, the individual teeth being more conspicuous. The whole outer surface of the jaw near to its working edge is covered by a sort of tesselated pavement, formed by the several teeth which are pressed together into a mass, but they form only the outer surface and the immediate edge, so that the soft bone forms a part of the working surface, or would do so but that, by its more speedy wear, it leaves the edge, formed by dentine and enamel, always prominent and more or less sharp.

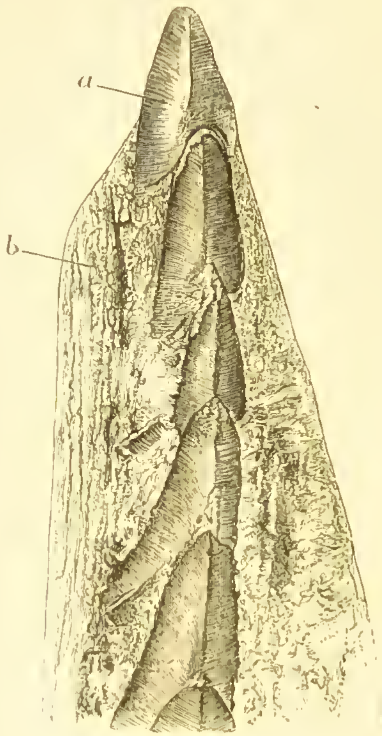
The structure and succession of these teeth have been carefully described by J. von Boas (Zeits. f. Wissen. Zool. xxxii), and the differences between the several genera pointed out. He describes cementum as binding the denticles together and forming a part of the working edge, but that which he describes as cementum appears to me to be that tissue which I have termed "bone of attachment." See page 220.

In a section of a jaw in my possession, which I believed to have belonged to a Gymnodont fish but which bears a remarkably close resemblance to that figured by von Boas as being a jaw of Pseudoscarus, a very beautiful arrangement serves to preserve the sharpness of the edge of the jaw.

The denticles are conical, and form a series of hollow superimposed cones with the points upwards; they consist

of dentine and enamel, and the point of the subjacent cone fits closely up into the hollow of that above it, so closely that in von Boas' specimen the dentine of the older tooth is in great part absorbed (?) to make way for the point of its

FIG. 105 (1).

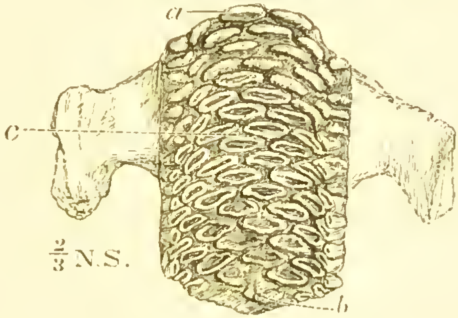


successor, so that the working denticle comes to be little more than a hollow cone of enamel. This is not the case in my specimen in which there is a quantity of dentine left in each denticle. This vertical series of superimposed sharp cones lie in the midst of the somewhat thin jaw bone, fused together by cementum (? bone of attachment), and enclosed between the inner and outer plates of the jaw.

(1) Edge of jaw of Pseudoscarus (?) *a.* Denticles. *b.* Bone of jaw

The bone being much softer than the denticle, wears down much faster, so that the edge is always formed by a prominent sharp tooth, which, as the wearing down of the bone progresses, falls off, and the next one beneath it comes into play. The arrangement recalls the way in which a scythe or a chisel is assisted in keeping its edge by being made of a plate of steel welded between two plates of softer iron.

Fig. 106 (1).



The pharyngeal bones are also remarkable; the two lower are united into one, and the stout bone so formed is armed with teeth; it is antagonised by two upper pharyngeal bones similarly armed. It carries teeth which are anchylosed to it, and which are so disposed as to keep the surface constantly rough. When they are freshly formed the teeth have flattened thin edges, something like human incisors. The teeth are coated with enamel, and thus, when calcification has proceeded so far as to obliterate their central pulp cavities, after the tooth is worn to a certain point (*c* in Fig. 104) it presents a ring of enamel, inside which comes a ring of dentine, and inside this a core of secondary

(1) Lower pharyngeal bone of Pseudoscarus. *a*. Posterior border, at which the teeth are unworn. *c*. Oval areas formed by teeth, the points of which are worn off. *b*. Anterior edge of bone, at which the teeth are almost completely worn away.

dentine, as seen in the figure. Owing to the different hardness of the three tissues a eonstant roughness of surfaee is maintained. The upper pharyngeals are similarly armed; and as the teeth and the supporting bone wear away, fresh teeth are developed at the front, so that the whole bone undergoes a sort of gliding motion baekwards, the armature of the lower pharyngeal being renewed in a similar manner, save that new teeth and bone are developed at its posterior instead of its anterior extremities.

The teeth are developed in bony erypts, beyond the youngest funetional teeth, and perforations in the roofs of the erypts give passage to the eonneeting band between the tooth sae and the mueous membrane.

No more fitting plaee will oeeur for notieing the stout pharyngeal teeth whieh are met with in so many fish. Some fish, whieh are edentulous so far as the mouth proper is eoneerned, have the pharyngeal bones armed with teeth; in the earp and its allies, edentulous so far as the mouth proper is eoneerned, the two lower pharyngeal bones earry long pointed teeth, whieh partly oppose one another, and partly oppose a sort of horny tuberele, whieh is supported on a proeess of the base of the oeeipital bone.

A few fish are quite without teeth; the sturgeon, whose mouth forms a protrusible sueker, is edentulous, as are also the pipe fish, and the little sea horse (Hippoeampus), now so common in aquaria.

But as a rule fish are remarkable for the great number of their teeth, which are being eonstantly shed off and replaeed by sueeessors an indefinite number of times.

In all the fish hitherto mentioned in these pages, it happens that the teeth in different parts of the mouth differ in size and in the funetion whieh they have to perform; but this is only so beeause a few striking forms have been naturally seleeted for deseription. It is far commoner for all the teeth of a fish, partieularly of those fish whieh have

countless numbers of teeth, to be very nearly alike in form and size in all parts of the mouth. As a general rule, fish do not comminute their food very fully, but make use of their teeth simply for the prehension of prey, not submitting the food to any mastication whatever; their teeth are hence often mere sharp cones, slightly recurved, or set looking backwards. Thus, though the mouth of the common pike is beset with an immense number of sharp teeth, its food is swallowed whole, and very often is alive when it reaches the stomach, the sole purpose served by the teeth being the prevention of its escape when once it has been seized.

Implantation of the teeth in sockets is not usual in the class of fish, but it does occur; for example the Barracuda pike (Sphyræna) has its lancet-shaped teeth implanted in distinct sockets, to the walls of which they are said to become slightly anchylosed; the file-fish and others might also be cited. And although the succession of teeth is usually from the side, in some cases the successional teeth are developed in alveolar cavities within the substance of the bone, and displace their predecessors in a vertical direction, as happens in the pharyngeal teeth of the Wrasses, or the curiously human-looking incisors of the Sheep's head fish (Sargus); the Lepidosteus also has its teeth affixed in incomplete sockets, to the walls of which they are anchylosed; this is not a very uncommon arrangement with the teeth of fish when they are socketed at all.

It is not common for sexual differences to be met with between the teeth of the male and female, though a slight difference exists between the sexes in some species of Skate. And although not strictly speaking a dental character, it may not be out of place to mention here the peculiar armature of the jaw of the male Salmon at the breeding season.

The end of the lower jaw becomes produced, and turned

upwards at its point; the stout cartilaginous hook thus formed is of such dimensions that it has to be accommodated during closure of the mouth in a deep cavity formed for it between the intermaxillary bones. In some Canadian salmon this process is supposed to be constant in the older males, but in the British fish it disappears, and only exists at the breeding season. A fish in which it is strongly developed is a foul fish, and is called a Kelt. It is used apparently as a battering ram, and such salmon are constantly found killed, with their sides deeply gashed by the charges of their opponents.

Not much can be said in general terms of the structure of the teeth of fish. The bulk of the teeth of most fishes is made up of one or other modification of vasodentine or osteodentine; this is often glazed over upon its exterior by a thin film of enamel, so thin as often to appear structureless.

Unvascular dentine also forms the teeth of many fish, and in some is remarkable for the fineness of its tubes; in fact, every form of dentine, from fine-tubed hard dentine to tissue indistinguishable from coarse bone is to be found in this class.

Dentine of very complex structure (labyrintho-dentine) is met with in some fish; and an example from the Lepidosteus (American garpike, a ganoid fish) has been figured at page 82.

Enamel is often present in a very thin layer, glazing the exterior of the dentine (see Fig. 49); sometimes it forms a mere tip, a sort of spear-point to the tooth as in the Eel and the Hake (see Figs. 93 and 89), and sometimes it is very thick, and itself permeated by systems of tubes (see Fig. 25).

Cementum is of comparatively rare occurrence in fish.

Professor Kölliker has shown that in a very large number of fishes the skeleton more nearly resembles dentine than

true bone in its structure; whilst the dermal scales and protective spines of fish are often made up of a tissue much resembling dentine (cf. Professor Williamson, Philos. Trans. 1849). We may say, then, that just as in the external skin, bony or dentinal plates are developed for the purpose of protecting it from destruction by attrition, so for a similar purpose teeth are developed in that portion of the mucous membrane which covers the jaws.

CHAPTER VII.

THE TEETH OF BATRACHIA AND REPTILES.

In these classes the teeth are never so numerous nor so widely distributed upon the bones of the mouth as in fish; a double row of teeth arranged in concentric lines in the upper jaw, between which a single row of teeth upon the lower jaw passes when the mouth is closed, is an arrangement rather common amongst Batrachia. The outer of the two rows of teeth in the upper jaw is situated upon the premaxillary and maxillary bones, and usually extends further back than the vomerine or inner row. Almost all Batrachians and Reptiles have an endless succession of teeth; but there are a few lizards (*e.g.*, Hatteria), in which the manner of succession, if there be any, has not been definitely ascertained.

From this type of dentition there are many deviations; thus the toads are edentulous, and the frog has no teeth in the lower jaw.

The teeth of the frog form a single row upon the margin of the upper jaw, their points projecting but little above the surface of the mucous membrane, and the vomerine teeth are few in number and cover only a small space.

The edentulous lower jaw passes altogether inside the row of upper teeth, and, having rounded surfaces and no lip, fits very closely against the inner sides of the teeth. Thus it leaves very little room for the young developing tooth sacs, which are accommodated with the space required for

the attainment of their full size, by the absorption of the older solid bone and the tooth which has preceded them, in the following manner. The teeth are attached to the bone by anchylosis, each tooth being perched upon a little pedestal of bone which is specially formed for it; and the successional teeth, the germs of which originally lay at the inner sides of the old teeth, commonly undermine the side of the pedestals and the bases of the latter, and move bodily beneath them, so that the new tooth completes its development in what was once the pulp cavity of its predecessor.

The teeth of the frog consist of a body of hard dentine, coated with an exceedingly thin layer of enamel, the existence of which has been doubted by some writers; but a study of the tooth-sac of the animal renders it probable that the transparent layer which is undoubtedly there is really enamel.

The teeth of the newt and its ally the salamander are remarkable for having tips of enamel, somewhat like those of the eel (see Fig. 93), save that they are bifurcated, the one point being larger and longer than the other.

The tadpole has its jaws armed with tough horny plates something like a turtle's bill, which are shed off, prior to the development of any true teeth; at all events I have myself been unsuccessful in discovering any tooth germs at the period when its horny bills are still in use, but Dr. Beard states that the horny teeth of amphibian larvæ are secondary developments.

Some extinct batrachia were of large size; the Labyrinthodon, the structure of whose teeth has already been described (page 85), was furnished with a marginal row of teeth in the upper jaw, of which some few were of larger size and greater length than the others. In the lower jaw, the teeth, which are similar to those of the upper, are disposed in some sense in an incomplete double row, the

series of smaller teeth not being interrupted by the occurrence of the larger tusks, but passing in unbroken series outside them. The Labyrinthodon was possessed also of palatine teeth.

The teeth were anchylosed to slight depressions or sockets, and the successional teeth were probably developed, as in the frog, at the inner side of the bases of the teeth already in position, as there are no indications of crypts within the bone.

In many reptiles teeth are developed for the merely temporary end of effecting an exit from the egg-shell. This purpose is sufficiently answered by the hard snout of the crocodiles, and by a sort of snout developed in CHELONIA, but snakes and lizards have sharp teeth, which afterwards are lost, developed on the premaxillary bones (Owen).

The CHELONIA, comprising the Tortoises and Turtles, have no teeth, but the margins of the jaws are sheathed in horny cases, which are variously shaped in accordance with the habit of the animal, being sharp and thin edged in carnivorous, and blunt and rugged in herbivorous species.

SAURIAN reptiles (lizards, &c.), have, as a rule, rather simple teeth, which are confined to the margin of the jaws, the occurrence of palatal teeth being less usual. The teeth are of various forms, being blunt and rounded in many genera, whilst in others they are long and pointed. They are generally made up of a central body of hard dentine, more or less completely invested by a cap of enamel; and they are attached to the bone by anchylosis.

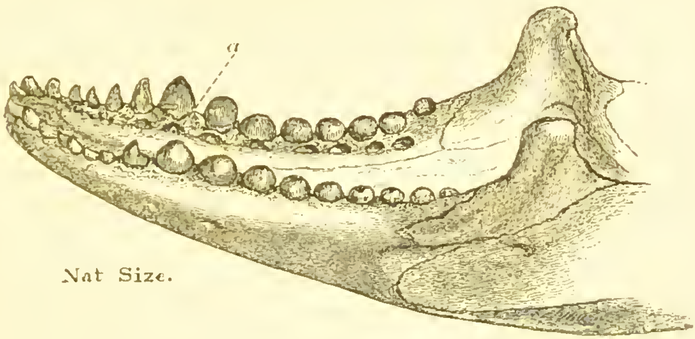
When the tooth is anchylosed by its outer side to an external parapet of bone, the creature is said to be "pleurodont," when by the end of its base it is attached to the summit of a parapet it is "acrodont."

The succession of teeth in the Lizards is constant, new teeth being developed at the inner side of the bases of the old teeth, which become undermined by absorption and fall

off when the successional tooth has attained to a certain stage in its development.

The accompanying figure of the lower jaw of a Monitor lizard will give an idea of a dentition common in the group. The teeth are not very large nor very numerous, there being about 30 in the jaw; towards the front of the

FIG. 107 (1).



mouth they are a little more pointed than at the back, but the differences in this respect are not striking.

At the inner side of the bases of the teeth are seen foramina which lead into the spaces in which new teeth are being developed.

Amongst the lizards considerable variety in the form of the teeth themselves exists, some having thin serrated edges, others being exceedingly blunt and rounded, but in the general disposition of the teeth there is considerable uniformity.

The teeth of some lizards consist at their apices of ordinary hard dentine, with a simple central pulp cavity, but at their bases of plicidentine with numerous subdivisions of the pulp cavity, as is seen in the Monitor lizards (Varanus, see p. 83). One Mexican lizard (Helodermus) has the re-

(1) Lower jaw of a Lizard (Varanus Gouldii). *a*. Foramina leading to cavities of reserve

putation of being poisonous, and has teeth which are grooved both back and front; but it is doubtful whether its harmful powers have not been exaggerated. In Heloderma the salivary glands of the lower jaw, probably the submaxillary glands, lie close against the under side of the bone. In a dissection made by Professor Stewart upon a specimen in the College of Surgeons museum, there appear to be a number of ducts which seem to actually perforate the bone, and they emerge by series of little holes which lie in the sulcus between the lip and the teeth, close to the necks of the teeth.

In the Python the corresponding gland also has many ducts which open in a similar position, but they attain to it without any perforation of the bone, and there is no reason to suppose that their secretion is at all poisonous; in the case of Heloderma there is, however, no doubt that the secretion is poisonous; indeed the bite of a specimen in the Zoological Gardens has been found to be fatal to small animals, and Dr. Weir Mitchell states that in one instance it is known to have been fatal to man. It is, however, a creature of gentle disposition, and it is not at all easy to make it bite.

Vaso-dentine occurs in the teeth of some saurians, as for example, in those of the great extinct Iguanodon, in which it, roughly speaking, formed the inner half of the crown, the outer moiety consisting of hard dentine. In addition to this peculiarity, the teeth of Iguanodon were remarkable for the partial distribution of the enamel, which was strongly ridged, the ridges being serrated, and was confined to the outer side of the crown. Thus at the outside came the hardest tissue, the enamel; next the harder dentine, and on the inside, the softer vaso-dentine. Hence, as the tooth wore down, a sharp edge was long preserved.

There is a New Zealand lizard, to which the several names of Hatteria, Sphenodon, and Rhyncocephalus have been given,

which has a very peculiar dental armature (Dr. Günther, Phil. Trans., 1867).

The intermaxillary bones are armed with two teeth, so large as to be co-extensive with the whole bone in width, and of a form which recalls that of the gnawing incisors of Rodents; the other teeth are quite small, and "acrodont" in their attachment.

But the great peculiarity of Hatteria is that the alveolar margins of the jaws are sharp, and when the teeth are worn down, which would happen in adult specimens, the actual sharp margins of the bone come into play as masticatory organs, near to the front of the mouth. It occurred to me as probable that the surface thus exposed might be coated with dentine, but a microscopic examination of one of the specimens in the British Museum, which I was, by the kindness of Dr. Günther, enabled to make, proved that the dense ivory-like surface which serves the purposes of mastication is true bone, and has no relation to dental structure.

There are very few other instances of actual bone, uncoated by dental tissues, being used for masticatory purposes.

The great extinct Dicynodon, an African fossil, also had sharp trenchant margins to its jaws; it is not known whether these were sheathed in horny cases like those of the turtles, or whether the bones themselves came into use, as in Hatteria. But the most striking peculiarity of Dicynodon was the co-existence with such jaws of a pair of very large caniniform tusks, a thing very unusual in the reptilian class, extending downwards and forwards from the upper jaw, and growing from persistent pulps.

The dentition of **Ophidian** reptiles (snakes) is very uniform; they may be conveniently divided into two groups, the poisonous and the non-venomous snakes.

Non-venomous snakes have one row of teeth in the lower jaw, and two rows in the upper jaw; in the latter the

maxillary bones carry one row, while a parallel internal row is supported upon the palatine and pterygoid bones.

The teeth are in both groups strongly recurved, and are firmly anchylosed to the bone; they consist of a central body of unvascular dentine, coated by a very thin layer of enamel (there is not, as is generally supposed, any layer of cementum, the enamel having been erroneously supposed to be such).

The two halves of the lower jaw are connected at the symphysis by an exceedingly elastic ligament; their articulation with the base of the skull through the medium of an elongated movable quadrate bone, is also such as to allow of their being widely separated from the skull and from one another, which allows of the dilatation rendered necessary by the large size of the creatures which a snake swallows whole.

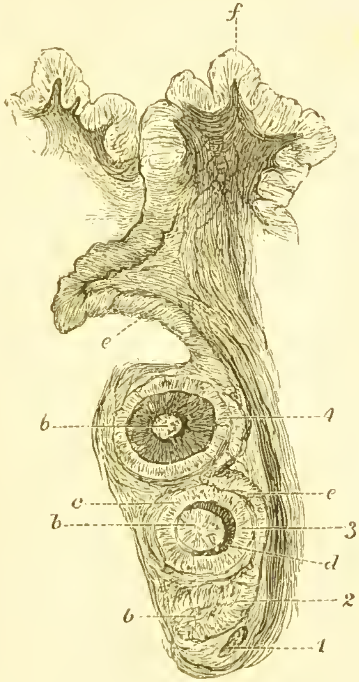
The teeth of the snake are simply available for seizing prey and retaining it, as the snakes invariably swallow their prey whole, and in no sense masticate it.

As the object to be swallowed is often so disproportionately large as to make the process of deglutition appear an impossibility, the mouth and pharynx have to undergo great dilatation. The arrangements which combine to give to the lower jaw its mobility have just been alluded to; the successional tooth germs, which are very numerous, are also arranged in the snake in an unusual position, which by bringing them very close to the surface of the bone, to which they lie parallel, renders them less liable to displacement and injury than they would have been had they been placed vertically, as they are in all other creatures; while in addition to the advantage of protection by position, they are wrapped round by a sort of adventitious capsule of connective tissue.

As the teeth during their development are thus lying down parallel with the length of the jaw-bone, when the period for their replacing a predecessor arrives, they have not only

to move upwards, but also to become erected; how this is done remains a mystery, for I have been quite unable to discern the means by which it is accomplished.

Fig. 108 ([1]).



When a snake has seized its food, which it retains by means of its many sharp recurved teeth, it slowly swallows it by advancing first its lower, then its upper jaw, till it thus, so to speak, forces itself over the body of its prey. When this latter is large, deglutition is a very lengthy process, but an English snake can swallow a moderate-sized frog with considerable rapidity.

([1]). Developing teeth of a Snake. *f.* Oral epithelium. *e.* Neck of the enamel organs. *b.* Dentine pulp. *c.* Enamel cells. *d.* Dentine. 1, 2. Very young germs. 3, 4. Older germs.

There is an African snake (Rachiodon) which has none but rudimentary teeth; its food consists of eggs, which thus escape breakage until they reach the œsophagus, into which spinous processes from the under surface of the vertebræ project, and there serve to break the egg; snakes with their dentitions similarly modified exist also in India (e.g., Elachistodon).

Fig. 109 [1].

It has already been mentioned that the non-venomous snakes have two complete rows of teeth in the upper jaw, the outer row being situated on the maxillary bones, the inner upon the palatine and pterygoid bones. The teeth of such snakes as the Pythons are all simple recurved cones,

[1] One half of the skull of a Python (without the lower jaw) seen from below. *a.* Intermaxillary bone. *b.* Maxillary bone, carrying the outer row of teeth. *c. d.* Palatine bone and pterygoid bone, the teeth upon which constitute the inner or second row of teeth.

and are none of them either grooved or canaliculated.[1] Some of the harmless snakes, however, have particular teeth which are developed to a greater length than the rest, and others have the posterior teeth on the maxillary bones grooved; but the statement that this grooving serves to convey an acrid saliva into the wound inflicted rests on insufficient foundation. The poisonous snakes are characterized by a shortening of the series of teeth carried upon the maxillary bone, and by the front teeth of the series being developed to much greater length than those which lie

Fig. 110 (2).

behind it. Thus Hydrophis, a genus of poisonous sea-snakes, has five or more teeth upon the maxillary bone, the foremost of which is much the largest, and this largest tooth is so deeply grooved upon its anterior surface as to be converted into a tube, the tube serving to convey the poison into the wounds inflicted by it.

(1) It has been proposed to divide the Ophidia into groups, distinguished by the presence or absence of grooved teeth, thus :—

i.	*Aglyphodontia.*	No grooved or canaliculated maxillary teeth.
ii.	*Opisthoglyphia.*	Some of the posterior maxillary teeth grooved.
iii.	*Proteroglyphia.*	Anterior maxillary teeth grooved. Posterior maxillary teeth solid.
iv.	*Solenoglyphia.*	Maxillary teeth few, canaliculated—poisonous snakes.

(2) Head and jaws of Hydrophis. The maxillary bone (*b*), instead of carrying a complete series of teeth, is armed with a few teeth only near to the front. The foremost tooth is canaliculated, and forms the poison fang.

Poisonous snakes which have several teeth upon the maxillary bone for the most part present some little external resemblance to the harmless snakes, and are called "colubrine poisonous snakes" (coluber being the name of a genus of harmless snakes); they present transitional characters between these and the more specialised or "viperine" poisonous snakes. The Cobra is a familiar example of a colubrine poisonous snake, and almost all the venomous snakes of Australia belong to this group. Their poison fangs are not very long, and they remain constantly erect, the maxilla to which they are anchylosed not being movable, as in the viperine snakes: it also carries a varying number of small insignificant teeth behind the poison fang.

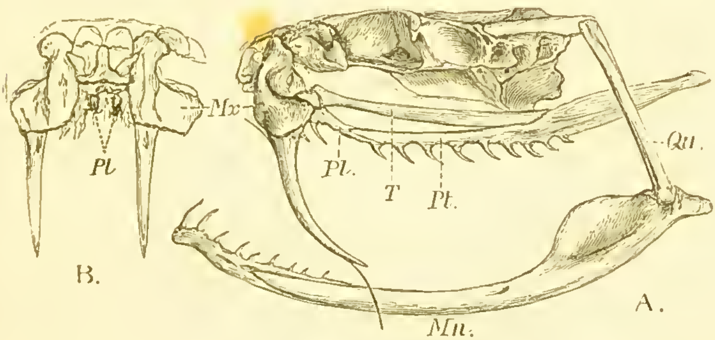
In the viperine poisonous snakes (Puff-Adder, Rattlesnake, Vipers, &c.,) the poison apparatus is yet more specialised. The maxillary bone carries no teeth at all behind the poison fang; it is so reduced in length as to be of squarish form, and is so articulated to the skull as to be movable.

The poison fang is of great length, so that if constantly erect it would be much in the way; when it is out of use, however, it is laid flat along the roof of the mouth, and is only erected for the purpose of striking; when in repose it is altogether hidden by a fold of mucous membrane, which, when it is erected, becomes tightly stretched over a part of its anterior surface, and serves to direct the poison down the poison canal by, to a great extent, preventing its escape around the exterior of the tooth.

The mechanism by which the poison fang is erected is thus described by Professor Huxley (Anatomy of Vertebrated Animals, p. 241):—"When the mouth is shut the axis of the quadrate bone is inclined downwards and backwards. The pterygoid, thrown back as far as it can go, straightens the pterygo-palatine joint, and causes the axis of the palatine and pterygoid bones to coincide. The trans-

verse, also carried back by the pterygoid, similarly pulls the posterior part of the maxilla and causes its proper palatine face, to which the great channeled poison fangs are attached, to look backwards. Hence these fangs lie along the roof of the mouth, concealed between folds of the mucous membrane. But when the animal opens its mouth for the purpose of striking its prey, the digastric muscles, pulling up the angle of the mandible, at the same time thrust the distal end of the quadrate bone forwards. This necessitates

Fig. 111 (1).



the pushing forward of the pterygoid, the result of which is twofold: firstly, the bending of the pterygo-palatine joint; secondly, the partial rotation of the maxillary upon its lachrymal joint, the hidden edge of the maxillary being thrust downwards and forwards.

"In virtue of this rotation of the maxillary through about a quarter of a circle, the dentigerous face of the maxilla looks downwards and the fangs are erected into a vertical position. The snake 'strikes' by the simultaneous contrac-

(1) Side and front view of the skull of Craspedocephalus melas. A bristle is passed down the poison canal. *Mx.* Maxillary bones. *Mn.* Mandible. *Pl.* Palatine bones. *Pt.* Pterygoid bones. *Qu.* Quadrate bone. *T.* Transverse bone.

A. Side view. B. Front view.

tion of the crotaphite muscle, part of which extends over the poison gland, the poison is injected into the wound through the canal of the fang, and this being withdrawn, the mouth is shut, all the previous movements reversed, and the parts return to their first position."

The poison fang is a long, pointed, slightly recurved tooth, traversed by a canal which commences on its front surface, near to the bone, and terminates also on its front surface, a little distance short of its point; in the figure a bristle has been passed through it, and shows the points where it commences and terminates. This tube conveys the poison into the puncture, its upper orifice being in close relation with the end of the duct of the poison gland.

It has been mentioned that some snakes which have not definite poison fangs have a few of the large posterior teeth grooved upon their front surfaces, the object of this grooving being, as a matter of conjecture, to convey a more or less poisonous saliva into the wounds inflicted by them.

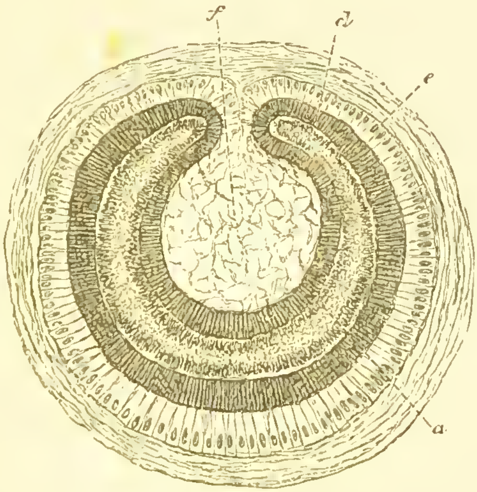
By imagining such an anterior groove to be deepened, and finally converted into a canal by its edges growing up and meeting over it, we shall have a fair conception of the nature of the tube in a poison fang, which is thus really outside the tooth; which might thus, at least in its canaliculated part, be regarded as a thin flattened tooth bent round so as to form a tube. Just as there are gradations in the armature of the maxillary bone, which link together the extreme form of the harmless Python, and the venomous Rattlesnake, so there are gradations in the form of the poison tooth, in the degree in which the groove is converted into a canal.

In colubrine poisonous snakes the canal is visible on the exterior of the tooth, where an apparent fissure marks the point where the two lips of the groove have met. Thus the poison fang of Hydrophis, although in a part of its length the canal is quite closed in, has a very marked line along

its front) and in section it looks much as would the dentine in Fig. 112, if the two cornua had their rounded extremities brought together into actual contact, without, however, their rounded outline being altered.

But in the poison fang of a viperine snake the lips of the groove are flattened and fitted to one another, so that not a vestige of the join can be seen upon the smooth exterior of the tooth. In the following figure the pulp cavity is

Fig. 112 (1).



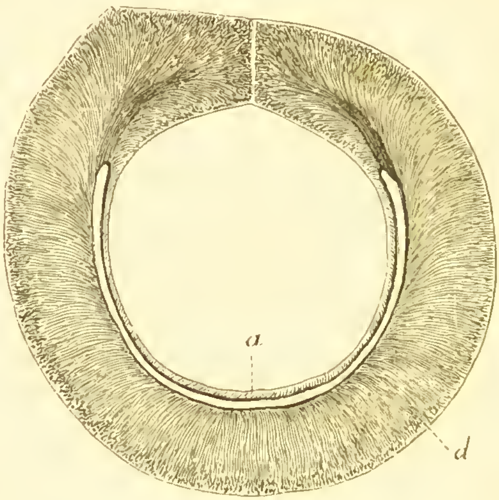
seen to be a thin flattened chamber partly surrounding the tube formed for the conveyance of the poison.

The poison-fang is exceedingly sharp, its point being continued some little distance beyond the place where the poison canal opens on the front of the tooth; this disposition of parts has been copied in the points of syringes for making subcutaneous injections.

(1) Transverse section of tooth-sac of poison fang of Viper, prior to the complete closure of the poison tube by the meeting together of the two cornua of the dentine.

The dentine is continued down to a very fine point, and it is cased by an exceedingly thin layer of enamel, not much more than $\frac{1}{600}$ of an inch in thickness in our common English viper: thus the utmost sharpness is secured, without loss of elasticity, which would have ensued had its point been made up of brittle enamel only. Enamel covers the whole exterior of the tooth but does not extend into the poison canal in the viperine snakes; in Hydrophis

FIG. 113 ([1]).



I believe that it does. As the point is simple, the tooth germ of a poison-fang only becomes distinguishable from that of another ophidian tooth after the tip of the tooth has been formed, when a groove appears in its side (see 8 and 9, in Fig. 114).

It being the habit of poisonous snakes to make use of these weapons to kill their prey, which they consequently do not swallow alive, it would obviously subject them to no little inconvenience to be without these weapons for

([1]) Transverse section of the poison fang of a Rattlesnake *a.* Pulp-cavity. *d.* Dentine.

any considerable length of time, while from their habit of striking living prey the long fangs must be very liable to being broken off by the jumping away of the creature struck, to say nothing of the great force with which the blow is given.

In the most typical (viperine) poisonous snakes the succession of teeth is conducted upon a plan which is unique, and which is excellently adapted to save loss of time in the replacement of a lost poison fang. Upon the movable maxillary bones there is space enough for two poison fangs, side by side; only one, however, is fully anchylosed to the bone at a time, and occupies a place to the extreme right or extreme left of the bone, leaving vacant space for another by its side.

When the tooth in use falls, it will be succeeded by a tooth upon the vacant spot by its side, not upon the spot upon which itself stood, so that the places on the right and the left of the bone are occupied alternately by the tooth in use. Thus in Fig. 111, the poison-fang of the snake's right side is seen occupying a position on the extreme outside of the maxillary bone, while its left poison fang is fixed on the inside of the maxillary bone.

The upper boundary of Fig. 114 is formed by the flap of mucous membrane which covers in the poison fang when at rest. Nos. 1 and 2 lie in the pouch formed by it, the section happening to be taken from a specimen in which the tooth was about to be changed. In most specimens one tooth only, the tooth actually in use, is seen in this position.

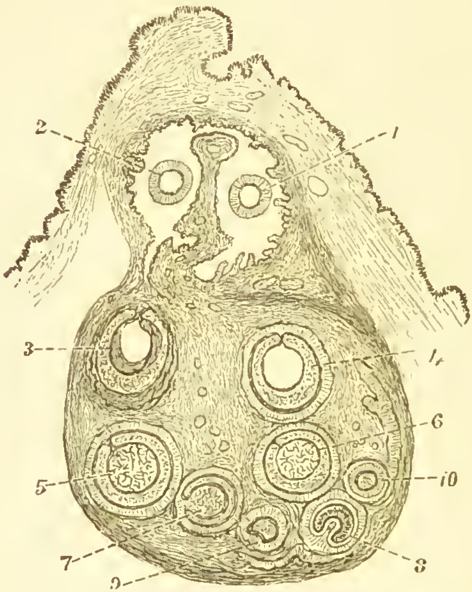
A flap hanging free across this space serves apparently to keep teeth of the one series from getting over to the other side, and probably serves to hold in place the reserve tooth when the older tooth is erected for biting.

The reserve poison fangs, as many as ten in number in the Rattlesnake, are likewise arranged in two parallel series, in which the teeth exist in pairs of almost equal age; the

tooth in use is thus derived alternately from the one and the other series, as is indicated by the consecutive numbers in the figure, a septum of connective tissue keeping the two series of teeth distinct from one another.

The teeth being arranged in pairs of almost equal age, suggest that the succession is both rapid and regular. All

FIG. 114 (1).



the reserve teeth lie recumbent in and behind the sheath of mucous membrane which covers in the functional tooth.

This arrangement of the successional teeth in a paired series does not exist in the Cobra, in which the successional teeth form but a single series; perhaps this may serve to explain the preference of the snake charmers for the Cobra,

(1) Transverse section of the reserve poison fangs of a Viper. 1. Tooth at present in use, in its recumbent position; were it erect, it would be withdrawn from view, or else seen in longitudinal section. 2. Tooth which will next succeed to No. 1. 3, 4, 5, &c. Tooth-sacs numbered in the order in which they will succeed.

which would probably take longer to replace a removed poison fang than a viperine snake would (1).

But in the colubrine venomous snakes the successional poison fang sometimes makes its way to a spot a little to the side of its predecessor, so that there may possibly be no loss of time; and notwithstanding that they are in a measure transitional forms between the harmless and the viperine snakes, some of them are most virulently poisonous and deadly in their bite (2).

This arrangement of *two* distinct chains of younger developing organs, all destined to keep the creature always supplied with *one* organ in a state of efficiency, is, so far as I know, without parallel.

Like other ophidian teeth the poison fangs become anchylosed to the bone which carries them, their secure fixation being aided by the base of the tooth being fluted, as well as by a sort of buttress work of new bone being thrown out to secure each new poison fang as it comes into place.

The poison is secreted by a salivary gland homologous with the parotid; by an especial arrangement of the muscles and fascia about it the erection of the poison fang and the infliction of the bite cause a copious stream of poison to be ejected. The duct terminates in a sort of papilla, close to the superior orifice of the tube in the fang; the passage of a considerable portion of the poison down the tube is secured

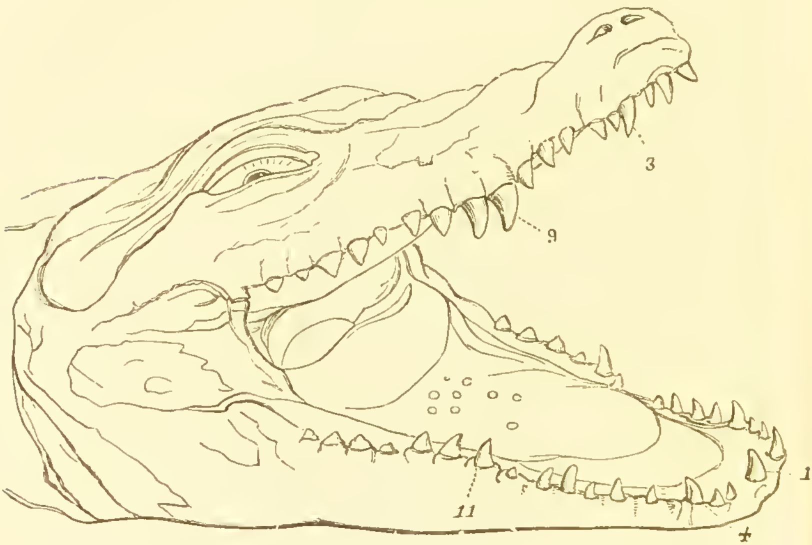
(1) An inquiry inserted in an Indian newspaper elicited the following answer:—"I have frequently seen snake-charmers exhibit snakes of the family *Viperidæ*, chiefly the Daboia Russelii and Echis carinata. I have also been told by some snake-charmers that they considered the Daboia even more poisonous than the cobra; and judging from the cautious way in which they handled these snakes—never lifting them off the ground without first putting a stick on their necks to hold them down—I feel pretty sure they all consider the vipers more dangerous than the cobras."

(2) I have given a more detailed account of the succession of poison fangs in the Philos. Trans., 1876, Part i.

by the close apposition of a shield of mucous membrane, which is strained over the erected tooth.

In **Crocodilia** the teeth are confined to the margins of the jaws, where they are very formidable in size and sharpness. The individual teeth are generally conical, sharply pointed, and often a little compressed from side to side, so

Fig. 115 [1].



as to possess sharp edges; but they vary much in form in different species.

The teeth are lodged in distinct tubular alveolar cavities, to the walls of which they do not become anchylosed, and they are tolerably constant in number in the same species.

In parts of the mouth certain teeth are developed to a greater length than those nearest to them; thus, in the Crocodile proper, the first and fourth lower teeth are spe-

(1) Jaws of the Crocodile. The first, fourth, and eleventh teeth in the lower jaw, and the third and ninth in the upper, are seen to attain to a larger size than the others.

cially large, while in the extinct African Galesaurus the difference is so marked that both in the upper and lower jaws the teeth might be grouped as incisors and canines, so far as size and probable function go in such a classification.

In structure the teeth of crocodiles consist of hard, fine tubed dentine, with an investing cap of enamel, and in ad-

Fig. 116 (1).

dition a coating of cementum on their implanted portions. As already mentioned, they are implanted in tubular sockets; new successional teeth are being continually developed at the inner side of their bases, and as these attain to a certain size, absorption attacks the base of the older tooth, and its successor moves into the space so gained, so that it comes to be situated vertically beneath the older tooth. In its further growth it causes yet more absorption

(1) Transverse section of the lower jaw of a young Alligator. *a.* Oral epithelium. *b.* Bone of socket. *d.* Dentine of old tooth. 2. Tooth next in order of succession, which is causing absorption of one side of the base of the older tooth. 3. Young tooth-germ.

of the older tooth, which it ultimately pushes out in front of it, sometimes carrying the remains of the old tooth like a cap upon its own apex when it first emerges. Each new tooth vertically succeeds its predecessor; hence no additional teeth are added, but the young newly hatched crocodile has as many teeth as a full-grown one.

In the extinct Ichthyosaurus the teeth, while forming an armature not unlike that of some of the crocodiles, were not implanted in distinct sockets, but were lodged in a continuous shallow groove, with but slight indications of transverse divisions.

The huge Dinosauria, some of which must have been thirty feet in length, had teeth implanted in imperfect sockets, the outer alveolar wall being considerably higher than the inner, and the transverse septa not very complete. The roots of the teeth were more or less perfectly cylindrical, and the enamelled crowns compressed and expanded, with trenchant edges. The tooth of the Iguanodon will serve as a fair example of a Dinosaurian tooth: the crown is greatly expanded, and presents anterior and posterior sharp notched margins; the enamel is laid over the outer surface of upper teeth, and the inner of lower teeth. The enamelled surface is ridged, so that as it wears down a notched edge is maintained. Moreover the maintenance of a sharp edge is further secured by the dentine on the enamelled side of the crown being of the hard unvascular variety, that on the inner being vasodentine and therefore softer. The remnant of the pulp ossifies, and comes into use, as these teeth remained at work until worn quite to a flat surface. The root portion was smooth, round, and curved.

Professor Marsh (American Journal of Science, March, 1880) has described and figured a peculiar Dinosaurian dentition, in a reptile to which he gives the name of Stegosaurus; the teeth are slightly compressed transversely, and are covered with a thin enamel; the roots are long and slender,

implanted weakly in separate sockets. But at the inner side of the roots of the teeth in use were no less than five successional teeth, in graduated stages of development, ready to ultimately take its place; so large a number of successional teeth has not hitherto been met with in a Dinosaur.

A very remarkable carnivorous reptile as large as a lion has been described by Professor Owen (Quart. Journal Geolog. Society, 1876,) under the name of Cynodraco major, for the reception of which he proposes a new reptilian order, that of Theriodontia. Its dentition is not completely known, but it possessed in the lower jaw eight incisors, of which the first is the smallest, and a canine of moderate size. The upper incisors are not known, but there were a pair of upper canines of such size that they extended down along the outside of a flattened portion of the lower jaw, like the canine teeth of Machairodus and those of Dinoceras. The hinder margins of these canines were trenchant, and finely serrated.

This protection of an especially long upper tooth by a corresponding down growth of the lower jaw is by no means an unusual provision of nature. Besides being met with in the instances cited, it is seen in Tinoceras, another of the Dinocerata, and in Chauliodus, a deep-sea fish dredged up by the "Challenger." It is, however, not a universal structure, as it is quite absent in the musk deer.

The **Pterosauria**, or flying reptiles, have, since the discovery of toothed birds, become of special interest to the odontologist. The wings were stretched membranes, like those of a bat, and the measurement across their tips in some of the largest must have been twenty-five feet; but most of those known were much smaller, from 10 to 15 inches in total length of body. In the Pterodactyls the jaws are furnished with long, slender, sharp teeth in their whole length; but in Ramphorhynchus the anterior extremities of

the jaws are without teeth, and it has been conjectured that these portions were sheathed in horny beaks.

And Prof. Marsh (American Journal of Science, 1876,) has discovered, in the same formation in which he found the toothed birds, several species of Pterodactyls wholly without teeth, for which the generie name Pteranodon is proposed.

The jaws, which are more like those of birds than those of any known reptile, show no traces of teeth, and the premaxillaries seem to have been encased in a horny covering.

THE TEETH OF BIRDS.

Prior to the discovery by Professor Marsh of Yale College, in 1870, of the remains of birds with teeth in the cretaceous formations of Western Kansas, little was with certainty known about the existence of teeth in any bird, although one or two fossils, leading to the suspicion that birds might have possessed teeth, were known. The state of knowledge up to that time has been clearly summarised by Mr. Woodward (Popular Science Review, 1875,) to this effect: that it had been long supposed that no examples of teeth were to be met with amongst the birds, although some, such as the Merganser, have the margins of the bill serrated, so that the functions of teeth are discharged by this horny armature of the jaws.

It is noteworthy that the margin of the bone of the jaws is also serrated, each serration corresponding to a similar serration in the bill. In the fossil bird described by Professor Owen, from the London clay, under the name of Odontopteryx toliapicus, the form of the bill is not known, but the margins of the jaws are furnished with strong bony prominences, far more conspicuous than those of the Merganser. And Geoffroy St. Hilaire had described a series of vascular pulps as existing on the margin of the jaw of

parroquets just about to be hatched, which, though destined to form a horny bill, and not to be calcified into teeth, yet strikingly recal dental pulps. Then there is also the famous fossil Archæopteryx, an anomalous oolitic bird, with a long and jointed tail, which is by many zoologists believed to have possessed teeth. There is a flaw in the evidence, however, inasmuch as the toothed jaw is not *in situ*, and therefore may possibly have belonged to some other animal than that perpetuated in the rest of the fossil impression, though probability is altogether in favour of its really belonging to the Archæopteryx.

In successive expeditions, conducted under great difficulties owing to the extremes of heat and cold, and to the hostility of the Indians, the remains of no less than one hundred and fifty different individuals referable to the sub-class ODONTORNITHES have been obtained by Prof. Marsh; they are classified under nine genera, and twenty species.

They are referable to two widely different types, one group consisting of comparatively small birds, with great power of flight, and having their teeth implanted in distinct sockets (Odontotornæ, illustrated by the genus Ichthyornis as a type); the other group consisting of very large swimming birds, without wings, and having teeth in grooves (Odontoleæ, type genus Hesperornis).

In Ichthyornis the teeth were about twenty-one in number in each ramus, all sharp and pointed, and recurved; the crowns were coated with enamel, and the front and back edges sharp but not serrated.

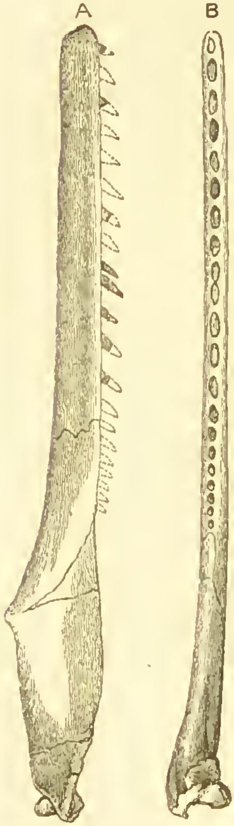
They are implanted in distinct though shallow sockets, and the maxillary teeth are a little larger than those opposing them; the pre-maxillaries were probably edentulous, and perhaps covered with a horny bill.

In the lower jaw the largest teeth occur about the middle of the ramus, those at its posterior end being materially smaller; and the sockets are deeper and stronger than in the

upper jaw. The succession takes place vertically, as in Crocodiles and Dinosaurs.

Fig. 117 (1).
1½ N.S.

A B



The genus Hesperornis, probably diving birds, includes species 6 feet in length : as has already been mentioned the teeth are not implanted in distinct sockets, but lie in a continuous groove like those of Ichthyosaurus ; slight projections from the lateral walls indicate a partitioning off into sockets, but nothing more than this is attained, and after the perishing of the soft parts the teeth were easily displaced, and had often fallen out of the jaws. The premaxillary is edentulous, but the teeth extend quite to the anterior extremity of the lower jaw : in one specimen there are fourteen sockets in the maxillary bone, and thirty-three in the corresponding lower ramus.

The successional tooth germs were formed at the side of the base of the old ones, and causing absorption of the old roots, migrated into the excavations so formed, grew large, and ultimately expelled their predecessors, as is seen in the accompanying figure.

In structure these teeth consist of hard dentine, invested with a rather thin layer of enamel, and having a large axial pulp cavity. The basal portion of the roots consists of osteodentine.

The outer side of the crown is nearly flat, the inner strongly

(1) Mandible of Ichthyornis (after Prof. Marsh). A. Side view, showing the teeth *in situ*. B. View of upper surface, showing the sockets in which the teeth were implanted.

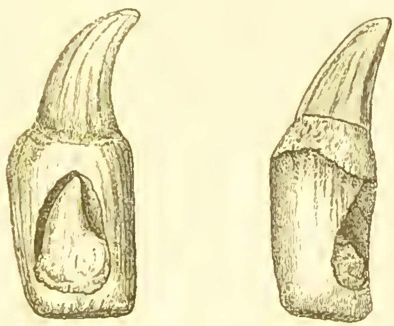
convex: the junction of these surfaces is marked by a sharp ridge, not serrated.

In form the teeth of Hesperornis present a close resemblance to those of Mosasaurus, a great extinct lizard.

Indeed, as Prof. Marsh observes, "in all their main features the teeth of Hesperornis are essentially reptilian

FIG. 118 ([1]).

A B

× 8  ½ N.S.

and no anatomist would hesitate to refer them to that class, had they been found alone. Combined with the other reptilian characters of Hesperornis . . . . they clearly indicate a genetic connection with that group."

In the dentine contour lines are abundant; the enamel is so dense as to appear structureless, and there is no coronal cementum.

The foregoing account is condensed from the magnificent volume published by the United States Government Geological Exploration. (Odontornithes, a monograph, &c., by O. C. Marsh, Prof. of Palæontology, Yale College.)

With these notable exceptions, the jaws of all known birds are toothless, the horny cases forming their beaks taking the places and fulfilling the functions of teeth.

([1]) (After Prof. Marsh.) A. Hesperornis regalis, with successional tooth in an excavation at its base; enlarged eight diameters. B. Tooth of Mosasaurus princeps, half natural size.

The evidence that true teeth may become replaced by horny teeth, these again coalescing with their neighbours to form a horny casing, has been given at page 44.

It would therefore seem possible that the ancestral birds all had true teeth, and it is possible that a sufficiently extended search might reveal rudimentary teeth surviving beneath the functional horny bill, or even possibly above it, like those of Ornithorhynchus.

CHAPTER VIII.

THE TEETH OF MAMMALIA.

The mammalia are usually now divided into three groups —**Prototheria, Metatheria,** and **Eutheria.**

The **Prototheria** comprise but few animals numerically, as no extinct forms are known, and of living animals only two families exist, namely, the Ornithorhyncidæ and the Echidnidæ. They stand at the bottom of the mammalian class, and present many points of affinity with lower vertebrates, particularly with Sauropsida and Batrachia.

Recent discoveries have added fresh interest to at all events the Ornithorhynchus, which has been found to lay eggs, and to be possessed of a unique arrangement of teeth.

Metatheria, like the preceding group, have characters which place them low in the mammalian scale, but they are numerously represented at the present day, comprising the animals known as Marsupials, which practically monopolize the Australian region, and exist also in the American continent. In former times they existed over other portions of the globe, and the earliest mammalian fossils are perhaps referable to the group.

Eutheria comprise all the mammals in whom the young are nourished by means of a placenta.

It must not be supposed by the student that the *Metatheria* of the present day are descended directly from the *Prototheria*, or that the *Eutheria* are direct descendants of the marsupials; it is more probable that exceedingly early and quite unknown mammalian forms have given rise to each of these

the marsupials a good deal, giving rise to a large number of forms, but that the *Eutheria* have far outstripped the others, and have been and are supplanting them in all directions.

It will be more convenient in this book to postpone the consideration of the marsupials till after the dentitions of placental mammals have been described.

PROTOTHERIA.

The Echidna is, so far as is known, entirely edentulous.

The Ornithorhynchus, which in its soft parts and skeleton alike differs from higher mammals in points which approach the characters of Sauropsida, is furnished with wide flattened jaws in which horny plates fulfil the function of true teeth; from this peculiarity comes its name of duck-billed platypus.

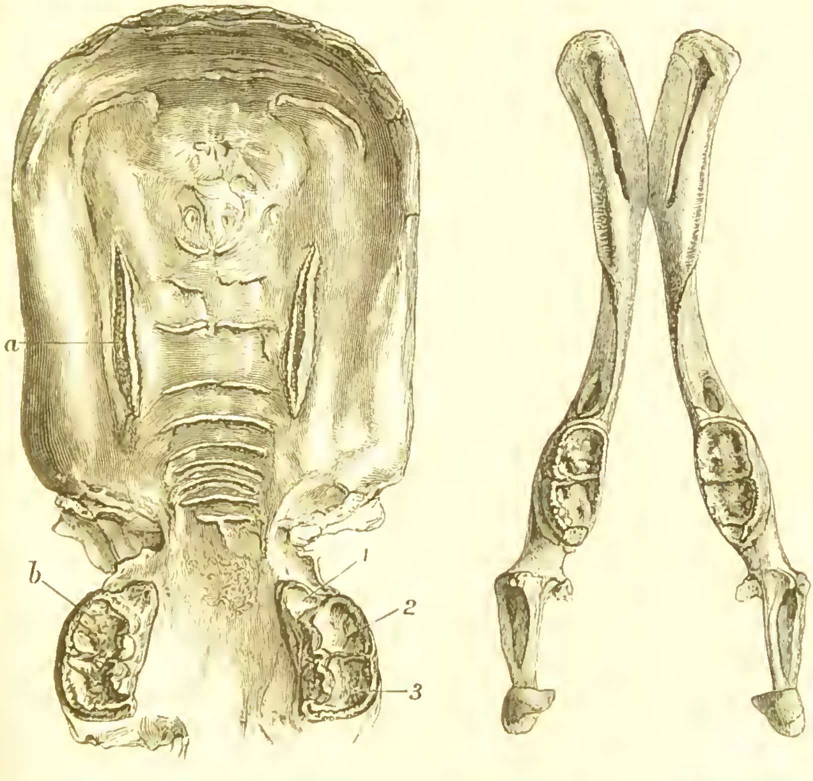
Recently Mr. Caldwell discovered that it, though possessed of functional mammary glands, lays eggs, and more recently still Mr. Poulton found that at an early stage tooth germs were present, as he supposed, underneath the horny plates. Following upon this Mr. Oldfield Thomas found that its true teeth came into actual use, and that they were not beneath, but above the horny plates.

To take first the dentition, if such it can be called, of the adult animals; the horny plates with which the jaws are ultimately furnished are four in number in each jaw, the anterior plate being a thin long band with a longitudinal ridge and a furrow in its inner side, and the posterior plate a flat broad-topped mass the surface of which is roughened by a series of ridges separated from one another by concavities, the ridges of the opposing plates interdigitating with one another.

These plates are simply pronounced thickenings and hardenings of the oral epithelium, and their under-surfaces are penetrated by long papillæ, each of which sends up a stems, and that the *Prototheria* have advanced but little,

prolongation of soft, deeply-staining, cells from its apex. The plates are at their sides quite continuous with the stratum corneum of the epithelium, of which their harder portions are composed; there is no calcification, and no bony structure in them. Somewhat similar horny structures occur upon their tongues.

FIG. 119 (1).



A full account of the structure and form of these plates will be found in a paper by Mr. Poulton ("Quart. Journ. Microscop. Science," Vol. XXIX., N.S.), which is devoted to a full description of his most interesting and significant

(1) Upper and lower jaws of Ornithorhynchus. From the lower jaw the skin, &c., has been removed, but it remains upon the upper. *a*. Anterior horny plate. *b*. Posterior horny plate, with remains of tooth sockets, 1, 2, 3.

discovery of the existence of the true tooth-germs which he believed to underlie the forming horny plates.

From the want of material he was somewhat uncertain as to the extent to which the calcification of these teeth goes, and what afterwards becomes of them, but he saw that there were the germs of four teeth in the upper, on each side, and probably the same number in the lower, jaw; and they occupy a widely open furrow, which he thought was subsequently occupied by the horny plate.

In this connection it is interesting to note that Professor Huxley, in writing of the Monotremes, had years ago expressed the conviction that there is good reason to suppose that edentulous forms are modified descendants of toothed forms.

Mr. Oldfield Thomas and Prof. Stewart subsequently found that the true teeth of Ornithorhynchus are cut, and for a time are in actual use; they are twelve in number, two on each side being of some size, and the third very small. The upper teeth have broad-topped crowns, with two long cusps on the inner edge, and a crenated border along the outer edge with many small cusps; in the lower this is reversed. They have low broad crowns with short stunted roots, by which, however, they are for a time pretty firmly held. Instead of being beneath the horny plates they are on the top of them, and their implantation is peculiar; the expanded crowns narrow rapidly at the neck, and they are surrounded by a very dense and thick epithelium, almost horny, which rises into a ring round them and dips underneath the expanded portion, so that the crown lies in a sort of cup of horny consistency.

This cup is not complete at the bottom, but the roots pass through it and fit depressions in the bone, which is perforated by foramina for their vessels and nerves. When the creature is about twelve inches long the teeth are shed, and then the horny cups grow in underneath and become complete; thus the curiously cupped and sculptured surface

of the horny plates which have been so long familiar has its form determined by once having formed the bed for a tooth with several roots, and although the horn grows underneath and fills up the holes for the roots to go through, yet the old general form is maintained by the horny plate which serves as the organ of mastication throughout the life of the animal.

FIG. 120 (1).

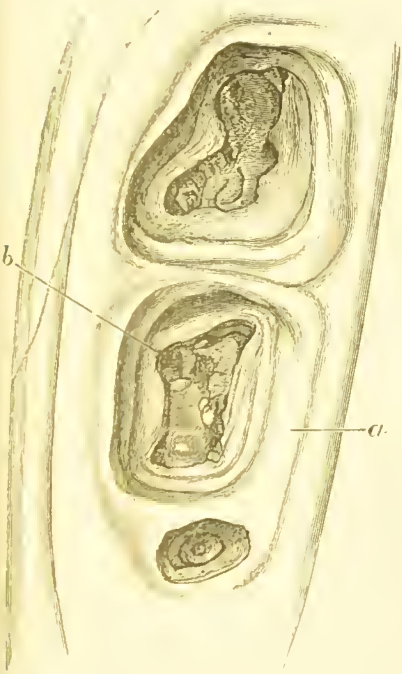
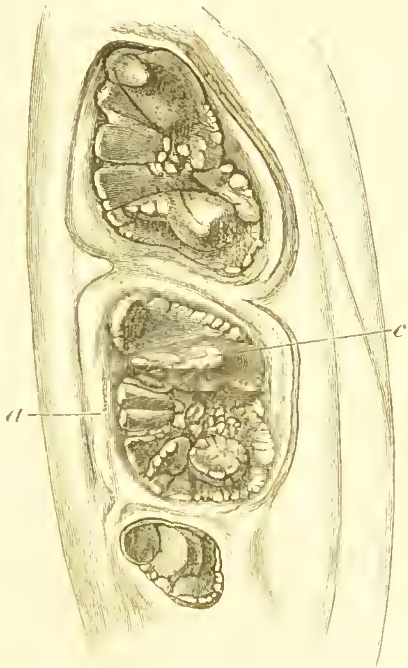


FIG. 121 (2).



So far as is known this is an arrangement quite unique amongst mammals, or indeed any other tooth-bearing creatures.

The horny plates are therefore not at all to be regarded as horny teeth, but they are epithelial structures which

(1) Horny plate, *a*, of a half-grown Ornithorhynchus, with empty pits; *b*, for the reception of the teeth.

(2) Horny plate with teeth in situ. *c*. Long cusp of tooth, after Prof. Stewart, from a specimen in the Royal College of Surgeons' Museum.

take the place of the teeth after these are shed, and therefore they are not closely homologous with the horny teeth of lampreys and myxinoids.

The true teeth consist of a body of dentine, with a central pulp cavity, capped with thin but hard enamel, and implanted by short roots, the breadth of crown greatly exceeding its vertical dimension.

The enamel is apparently of simple structure, and the dentine is permeated by fine dentinal tubes and beset with a wonderful number of interglobular spaces, which in parts of the crown mask its tubular structure. In the principal cusp larger, apparently vascular, canals exist, and as one approaches the stunted roots, a somewhat abrupt transition in structure takes place, all dentinal tubes disappearing, and large lacunæ appearing.

The roots are hence of softer, coarser material than the crown, which itself is not of a high type of dentine structure.

Fig. 122 (1).

Thus the dentine structure of the tooth is somewhat that which we are accustomed to see as a result of pathological processes, and would suggest, so far as it goes, that the Ornithorhynchus tooth has degenerated from some earlier and more complete tooth-form in which the roots were properly developed.

I am not acquainted with any example of this degeneration in the type of dentine formation as the root portion of the tooth is approached in any mammalian tooth: in those teeth

(1) Molar tooth of Ornithorhynchus. c. Long cusp.

which have no roots, if such an expression may be allowed, but which are about to become anchylosed to the bone, something of the kind may be seen (cf. also the tooth of Hesperornis, p. 280).

The British Museum specimen described by Mr. Oldfield Thomas (Proc. Roy. Soc., May, 1889), show that the teeth were subjected to severe attrition, as one which was about to be shed was worn as thin as paper. No tooth, fossil or recent, corresponds in naked-eye characters with that of Ornithorhynchus, though that of the mesozoic Microlestes does so in some degree, so that Mr. Oldfield Thomas gives a figure of it for comparison.

Microlestes has generally been looked upon as a mar supial, allied to Plagiaulax, and Prof. Cope has suggested that all the group of multituberculate toothed mesozoic mammals may have been monotremes.

But a microscopic examination of a tooth of Microlestes, which Mr. Poulton kindly allowed me to make, shows no close resemblance to the recent marsupials, for the ename is not clearly penetrated by dentinal tubes, nor does it present the peculiarities of structure found in Ornithorhynchus Thus its structure gives no help, but rather goes to render still more indefinite its probable zoological position.

But although these discoveries seem to carry us back to a form of mammalian tooth very remote in point of time, it has yet by no means a simple crown, and we are still very far from knowing anything which can be regarded as a primitive parent form whence all mammalian teeth may have been derived.

Still the discovery is of incalculable value, inasmuch as many of the early mammalia are known to us only by teeth, and the form and structure of a monotrematous tooth gives us something far lower in the evolutionary scale than had hitherto been known.

The Echidna, or scaly Ant-Eater, also an Australian mammal, has no teeth whatever, so far as is at present known.

EUTHERIA.

There is great difficulty in arranging Placental Mammals in any order of sequence, inasmuch as those now existing, and those fossil forms known to us, form but a small fraction of all which have once existed. And although no modern naturalist can well doubt that all existing mammals are lineal descendants of a smaller number of forms previously existing, yet they do not admit of being arranged on any one stem, and are not at all lineal descendants of one another.

Prof. Flower (art. Mammalia, Encyclop. Britannica) places them provisionally, and for want of a better arrangement, thus :—

Edentata—Sloths, Ant-Eaters, Armadillos, &c.
Sirenia—So-called Herbivorous Cetacea, Manatee, Dugong, &c.
Cetacea—Sperm Whales, Porpoises, Whalebone Whales, &c.
Insectivora—Hedgehogs, Moles, &c., &c.
Chiroptera—Bats.
Rodentia—Hares, Rabbits, Rats, &c.
Ungulata (Hoofed Mammals)—
  Hyrax—The single family Hyracoidea.
  Proboscidea—Dinotheriums, Mastodons, Elephants.
  Amblypoda—Great extinct animals from American Eocene formations, Dinoceras, &c.
  Ungulata vera—Perissodactyle Ungulates, Horse Tapir, Rhinoceros, &c.
    Artiodactyle Ungulates, Pigs, Camels, Ruminants, &c.
Tillodontia—A group of animals described by Profs. Marsh and Cope from American Eocene, with affinities to several groups, *i.e.* to Rodents and Carnivora, as well as to Ungulates.
Carnivora vera—Cats, Dogs, Bears, &c.
Carnivora pinnipedia—Seals, Walrus, &c.
Primates—Man, Monkeys, and Lemurs.

INTRODUCTORY REMARKS.

It was formerly customary to explain the various facts which were revealed by the study of comparative anatomy

upon the supposition that there was some sort of type or standard organization, and that all others were arrived at by modifications and departures from this type, these modifications being introduced with a direct purpose in view, in order to fit the creature to a special habit of life.

Among the matters which this "type" theory sought to account for was this: when an animal possesses some peculiar organ, it is found on close examination that it, however specialised, is after all only something which allied animals also possess, only it has been exaggerated or developed in an unusual manner and degree; or, on the other hand, that when an organ is wanting, the suppressed organ is not absolutely abolished, but is to be found stunted and in a rudimentary condition, instead of in its ordinary size and functional activity.

This is as true of teeth as of any other organs; indeed they afford many admirable examples of the law.

Thus the tusks of the boar or of the Sus babirussa, large and peculiar though they be, are not new developments, but are merely the canine teeth which in these species attain to unusual dimensions. In the same way the enormous straight tusk of the Narwal (see p. 343) is nothing more than an incisor tooth of one side, the fellow to which has been checked in its development; but this is not missing, for it remains throughout the life of the animal buried within its socket. In the female Narwal both of the teeth, being rudimentary, are permanently enclosed within the sockets, and are of course not of the smallest service to the animal, directly or indirectly; furthermore, as has been shown by Professor Sir W. Turner, in young specimens, a second pair of rudimentary aborted incisors are to be found, which in the adults have disappeared.

The modern school of biologists, rejecting the "archetype" theory refer these resemblances detected between dentitions upon the whole dissimilar to one another to a

more intelligible cause, namely, inheritance. Assuming, as the balance of evidence compels us to assume, that the many divergent forms which we observe have been derived by progressive modifications and differentiations from fewer ancestral forms, we shall have no difficulty in seeing how, by such processes as we full well know to occur, namely, the dwindling of disused organs and the exaggerated development of those very useful, great differences may ultimately result.

To illustrate what is meant by this so-called "adaptive modification," this suppression of things that are not needed, and increased development of those most used, we may recur to the dentitions of non-venomous and venomous snakes.

In these we saw, in the non-venomous snakes, the maxillary bones covered by a row of teeth sub-equal in size; then in the 'Colubrine' poisonous snakes the front tooth of the row standing upon the maxillary bone having taken upon itself a special and important office, namely, the conveyance into a wound of a poisonous saliva; coincidently with this tooth having attained its increased size and importance, the teeth behind it on the maxillary bone were reduced both in number and in size. Going a step further, to the Viperine poisonous snakes, the now useless small maxillary teeth have all disappeared, leaving the poison fang alone, of vastly increased dimensions, to occupy the whole bone.

But in many poisonous colubrine snakes the three or four small and useless teeth lingering upon the maxillary bone, though their function was gone, served to indicate to us in some measure the gradual process by which that singularly perfect adaptation of means to an end, the poison apparatus of the viper, was arrived at.

Mr. Darwin has proved that any modification in the structure of a plant or an animal, which is of benefit to its possessor, is capable, nay, is sure, of being transmitted and intensified in successive generations, until great and material

differences have more or less masked the resemblance to the parent form.

Just as man, by favouring the breeding of those modifications of form, &c., that please him best, has been able, in the course of a few years—in a length of time altogether infinitesimal, as compared with the time during which the surface of land and sea has been of pretty nearly its present form, to say nothing of the enormously longer earlier geological epochs—to profoundly modify the breeds of dogs, of horses, and of numbers of plants, all of which are absolutely known to have had a common origin, so in nature forces are and ever have been in perpetual operation, which effect the same thing.

A pigeon-fancier wants a pigeon of particular plumage, with a few feathers a little different from any pigeon he has ever seen or heard of (1); he knows by experience that little variations are for ever arising, and that by watching a sufficient number of young ones, and rigorously picking out those which at all tend in the direction of what he wants, he will get what he wants, and will even tell you with confidence that in so many years he will make a breed with the peculiarity desired. And exactly as the plumage that was wanted is got, so in nature the tooth that is "wanted," *i.e.*, the dentition that is excellently well adapted to do its work, by the operation of that law known as "survival of the fittest" may have been elaborated.

It is quite enough that one of the small variations for ever arising in animals shall be of advantage to it, for us to see how the peculiarity is likely to be transmitted and intensified in successive generations.

The question has been well presented by Mr. Wallace, who points out that we must not think so much of variations in individuals as in groups of individuals: for instance,

(1) An eminent pigeon-fancier, Sir J. Sebright, told Mr. Darwin that he could produce any given feather in three years.

it is a familiar fact that people vary in height, so that any hundred persons may be divided into fifty taller and fifty shorter persons. Now if a little extra height were of advantage, many or most of the fifty would experience it, though some might not. In the same way, if we grouped one hundred animals whose teeth varied a little in respect of strength into the fifty weaker and the fifty stronger, it is easy to see that the stronger fifty would get the better of the others in the struggle for existence on the whole, and would be more certain to propagate their kind, and would repeat in a majority of their progeny those peculiarities which had helped themselves to live.

Thus the doctrine of natural selection or survival of the fittest, is as fully applicable to the teeth of an animal as to any part of its organisation, and the operation of this natural law will be constantly tending to produce advantageous or "adaptive" differences. On the other hand, the strong power of inheritance is tending to preserve even that which in the altering conditions of life has become of very little use, and thus rudimentary teeth we may understand to be teeth which are in process of disappearance, having ceased to be useful to their possessors, but which are still for a long time lingering upon the scene. It was formerly supposed that the variations seized upon by natural selection and intensified in successive generations were of necessity small, so small that it was difficult to see how their advantage would really be felt.

But since attention has been drawn to this subject, and careful measurements and weighings have been taken of large numbers of wild specimens of the same species, it has been found that the variations are often far from being insignificant in extent.

Then Mr. Wallace (Darwinism, 1889) points out that the variation in common species reaches often 20 per cent. of the size of the part implicated, and this without reference to the

general size of the animal. As an example may be taken the jaws of the wolf, which in ten specimens varied to the extent of an inch and a half in length. If there be an advantage, it is easy to see how in a few generations a very distinct advance in the direction of length or shortness of jaw might be established.

Good examples of rudimentary teeth are to be found in the larval teeth of the edentulous sturgeon, or of the whalebone whales, or in the teeth buried beneath the horny plates of the deflected portion of the Dugong's jaw, all of these being of absolutely no service to their possessors. Some teeth have disappeared utterly; thus the upper incisors of Ruminants are gone, and no rudiments exist at any stage [1]; others still remain in a stunted and dwindled form, and do not persist throughout the life-time of the animal, as for instance the first premolars of a horse, or two out of the four premolars of most bears.

The teeth of Ornithorhynchus do work for their possessor till it approaches its adult size: then they are curiously supplanted by a horny development of the gums.

It must be borne in mind also that variability downwards will operate to slowly destroy an organ which is not being preserved by the action of natural selection.

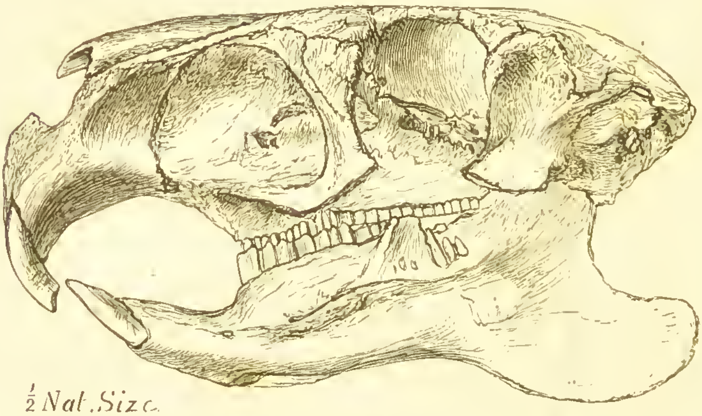
Before leaving this section of our subject, an instructive illustration of the operation of these agencies may be given

It is very easy for us to see how a "rodent" type of dentition is beneficial to its possessor by rendering accessible articles of food wholly unavailable for creatures which have no means of gnawing through a shell or other hard body. Now it happens that in three regions of the world, pretty completely cut off from one another, three animals, in parentage widely dissimilar, have arrived at dentitions of "functionally rodent" type.

(1) Statements to the contrary have been made, and copied from book to book without verification.

Thus in Australia, a region practically wholly monopolised by Marsupials, a marsupial, the Wombat, has a dentition very much like an ordinary placental Rodent. In the island of Madagascar, one of the very few parts of the globe without indigenous rodents (except a few Muridæ), a Lemurine animal, the Cheiromys, has a dentition modified in a

Fig. 123 ([1]).



½ Nat. Size.

similar direction, (though it is probably employed to get at a different sort of food); and elsewhere, scattered all over the world, we have the ordinary Rodents.

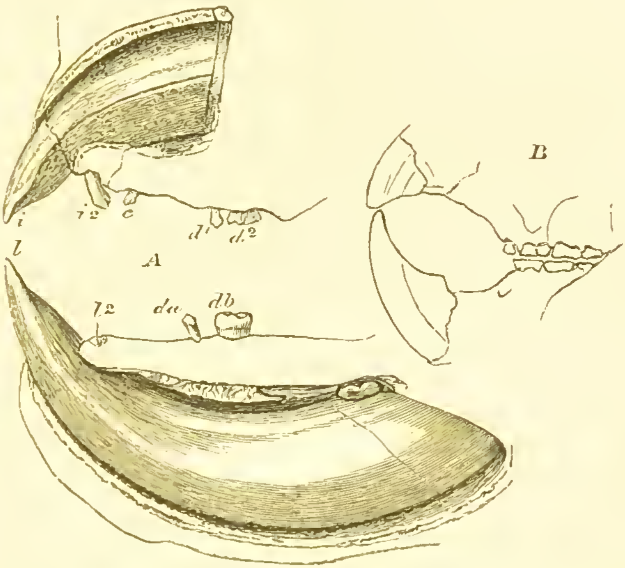
In fact, three sets of creatures, as widely different from each other in parentage as they well could be, have been modified by natural selection until they have dentitions, not identical, but for practical purposes not unlike.

It is impossible to conceive that these three creatures have had anything in the way of common origin: their ancestry must have been widely different, the regions in which they live have been isolated from one another for countless years, and yet they have each got to a "practically rodent" type of dentition. Of extinct Lemurs little is

([1]) Skull of a placental rodent (Capybara), showing general character of a rodent's dentition.

known, and of the ancestry of Cheiromys nothing; but in the compact group of Marsupials, still living in Australia, we are able to dimly see some of the progressive steps which seem to tend towards this rodent form of dentition. In Australia, roughly speaking, there were nothing but Mar-

FIG. 124 (1).



supials; in Madagascar more Lemurs than anything else; and in each case, out of the material at hand, natural selection has manufactured a "rodent" dentition.

At the same time the force of inheritance is seen in each of them retaining characteristics of the groups whence they have been derived, so that underlying the *primâ facie* resemblance in the teeth, there are points in their several

(1) A. Milk teeth of the Lemurine Cheiromys, with the permanent incisors just coming into place. It differs from any Rodent by having many milk teeth. *i.* Permanent incisor. *i* 2. Posterior deciduous incisor. *c.* Deciduous canine. *d*, *d* 2. Deciduous molars. *l.* Lower permanent incisor. *l* 2. Lower deciduous canine. *d a*, *d b*. Lower deciduous molar. B. Reduced outline figure of its permanent dentition, in which it closely mimics the true rodents.

dentitions whereby the wombat shows its marsupial affinities, and the Aye-aye its quadrumanous affinities.

An example of the same sort of thing is seen in the occurrence of hinged teeth in various families of fish (see p. 218) in which the requirements of a hinge and of a means for restoring the bent-down tooth to the upright position are attained by different mechanism according to the difference in the raw material, if such an expression may be allowed.

The approximation to a rodent type of dentition by a number of widely different animals has led to the suggestion being made, that it does not follow that all existing Rodents have had a common origin. Thus Oscar Schmidt ("Mammalia," Internat. Scientif. series, p. 291) writes :—"A comparison of the very different shapes of the molars in the Rodents among one another, and the approximation of many genera—not as yet decided Rodents—to the Rodent type (for instance the Wombat, the fingered animal (Aye-aye), and the rock coney) render it extremely probable that even our present Rodents are not of one and the same origin. The fact remains, animals of different derivation having attained a similar exterior, succeed extremely well in the struggle for existence, or even better in their endeavour to obtain food. Unlike as they may be, in one point they are incontestably alike, *i.e.* in the development of continuously growing incisors."

In addition to those modifications which are of direct use to the individual in the way of assisting in the procuring of food, &c., any character which would enable one male to get an advantage over other males, and so render him more certain to propagate his kind, will be sure to be transmitted and intensified.

Thus we can understand how the males of some species have become ornamented; how the males of many birds have come to sing; and, what is of more immediate concern to us, how the males of some animals have become possessed of weapons which the females have not. The possession of

weapons by the male is strikingly exemplified in the teeth of animals. The males of many frugivorous monkeys have canine teeth much larger than those of the females; they are cut late, coincidently with the attainment of sexual maturity, and are useful to their possessors as weapons in their combats with other males. The male narwal has its single elongated tusk; the male dugong has tusk-like incisors; in the respective females these same teeth are insignificant.

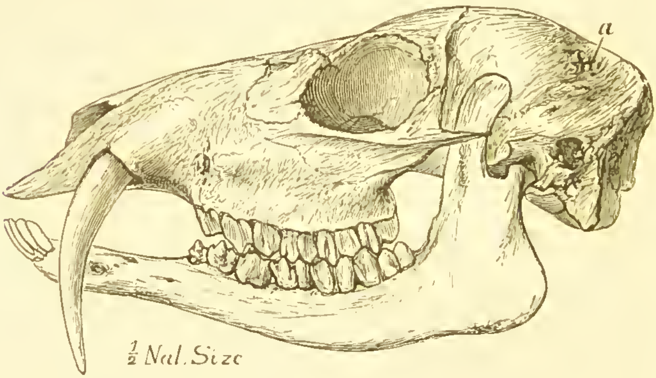
But the most striking instance of the teeth being modified, so as to serve as weapons for sexual combat, is afforded by some members of the group of ruminants, amongst whom, as Cuvier long ago pointed out, those which are armed with horns have no canine teeth, and *vice versâ*—a generalisation which, although subject to slight exceptions, remains upon the whole true.

The male musk-deer (Moschus moschiferus) has canine teeth of enormous length, while it is quite without horns (see fig. 125); the female has no canine teeth. The male muntjak, which has very short horns, has canine teeth, but of much smaller size than those of the musk-deer. Other examples of hornless deer furnished with canine teeth are to be found in Swinhoe's water-deer (Hydropotes inermis) and in the Elaphodus cephalophus (which has very small antlers) a Chinese deer more recently discovered, and in the Tragulidæ. It is obvious that males furnished with weapons more powerful than their fellows, will be more likely to prove victorious in their battles, to drive away the other males, to monopolize the herd of females, and so to transmit their own peculiarities to offspring, which will again be favoured in the same way. Thus it is very easy to see how, amongst gregarious animals, the development of teeth serving as sexual weapons is likely to be favoured, generation after generation, until canines as highly specialised as those of the musk-deer, or the wild boar, are attained to.

It will suffice to indicate to the reader that he must be

prepared to find that the teeth are profoundly susceptible of modification, but that, amid all their varied forms, the evidences of descent from ancestors whose teeth departed less from the typical mammalian dentition are clearly traceable in the existence of rudimentary teeth and other such characters. And, although it is by no means probable that we have recognised more than a part of the agencies which

Fig. 125 [1].



are at work, natural selection and sexual selection appear to be competent to produce most of the phenomena of modification observed. There remains one other influence, much more obscure in its nature, to be touched upon, namely, "correlation of growth" or "concomitant variation." When we find that when horns are developed, canine teeth are absent; or that, after a boar has been castrated, his tusks cease to grow, although we may be quite unable to conceive the precise manner in which the one thing influences the other, we can see that there is a consistency in the development of the sexual weapon ceasing coincidently with the destruction of the sexual apparatus, or in the fact that two kinds of weapon are not developed in the same animal.

[1] Cranium of Moschus, showing the long canine tooth.

But there are some correlations of growth of a still more recondite nature, in which the connection is less obvious. Of this nature is the relation which exists between peculiarities of the skin and of the teeth: the Edentata, abnormal in their skins, are different from most other Mammalia in their teeth; whales, yet more aberrant in the nature of their skins, have only rudimentary teeth, in the place of which, after birth, plates of whalebone are found.

Mr. Darwin ("Animals and Plants under Domestication,") has collected a number of curious instances of relations existing between hair and teeth. In general terms it may be said that any great abnormality in the hair goes hand in hand with an abnormality of the teeth. Thus, there is a breed of dogs found in Turkey which are almost hairless, and which have very few teeth, their dentition being reduced to a single molar on each side, together with a few imperfect incisors; and in the human subject inherited baldness has been often found to be associated with inherited deficiency of the teeth.

But we must not go further than to say, that great abnormality of hair goes hand in hand with abnormality of teeth, for examples have just been given of absence of hair and absence of teeth; and, on the other hand, redundance of hair has in several cases been accompanied by absence of teeth.

Thus, in the case of the now famous hairy family of Burmah, the peculiarity of silky hair being developed over the face was transmitted to a third generation, and in each case the teeth were very deficient in number. A year or two ago a hairy man and his son, said to have come from the interior of Russia, were exhibited in London, and they were also almost toothless.(1)

(1). The man's mouth exemplified the dependence of the growth of the jaw upon the presence of teeth. Ordinarily the increase in size between childhood and adult age takes place by a backward elongation, which allows for the successive development and eruption of the molars behind

A good many years ago a hairy woman (Julia Pastrana) was exhibited in London, of whom it has commonly been reported that she had an excessive number of teeth. Certain it is that her mouth was very prominent, and that she was described as "dog-faced" and "pig-faced," but models have been presented to the Odontological Society by Mr. Hepburn, which are indisputably known to be models of her mouth, and these do not show any excessive number of teeth. The teeth, at least such of them as can be seen, are enormously large, but the mouth is affected with general hypertrophy of the gums and alveolar processes to such a degree, that only a few of the teeth can be made out.

But this does not make her case the less interesting to the odontologist, for in the huge teeth, the enormous papillæ of the gum, and the redundant hairs on the face, we have evidence of a disposition to hypertrophies of the integument affecting in different places the different tegumentary appendages which happen to be there. And that the teeth are dermal appendages has been shown at a previous page (see page 2).

He would indeed be a rash man who ventured to assert that he had recognised all the agencies which are at work in the modelling of animal and vegetable forms; but it is safe to say that, at the present time, we are acquainted with "natural selection," or "survival of the fittest," an agency by which variations beneficial to their possessors will be preserved and intensified in successive generations; of "sexual selection," which operates principally by enabling those possessed of certain characters to propagate their race, while others less favoured do not get the opportunity of so doing; of "concomitant variation" between different parts

the space occupied by the temporary teeth. But this man never had any true molars, and no such backward elongation of the jaw had ever taken place, so that, though he was a full-sized man, his jaw was no larger than a child's.

of the body, an agency much more recondite in its operations, but by which agencies affecting one part may secondarily bring about alterations in some other part.

And operating in the contrary direction, we have a certain fixity of organization, so that the power of inheritance is constantly asserting itself by the retention of parts which have become useless, for a time at all events, and by the occasional reappearance of characters which have been lost.

Some rather contradictory statements have been made as to the direct effect of high feeding, improvement of breed, &c. upon the cutting of the teeth, early maturity being of course one of the aims of the improvers of farm stock.

With regard to horses, neither high feeding nor improved breed seems to have made any difference, *e.g.*, a Highland pony at five years has as full a mouth as the most pampered horse. But in cows it seems to be different—thus Highland cattle have all the permanent teeth at four-and-a-half or five years of age, whereas some improved breeds have a full mouth at three years (Williams, "British Dental Association Journal," April, 1882).

Prof. Brown ("Journ. Roy. Agricult. Soc.," 1881, where may be found much valuable information on this subject,) has been unable to trace any change in thirty years, though, if the older writers were accurate, a real acceleration has taken place over much longer periods.

He, however, quite denies that high feeding, of a litter of pigs for example, will produce any immediate effect, and strongly lays down that their dentition is a reliable test of age.

Even were it otherwise, there are many naturalists who, with Prof. Weissmann, think that acquired qualities, such as this would be, are never transmitted.

Allusion has been made to these great biological questions with the view of helping the student to have patience to master descriptions of minute points, of which he does not at the moment see the bearing, by giving him confidence

that there are no characters so trivial but that they may throw very important light upon the remote parentage and the line of descent of the creature under examination. And as a further incentive to painstaking and minute observation, it may be added, that things which are rudimentary, and therefore inconspicuous, are often just the things which happen to teach us most; for being of no present use, they are not undergoing that rapid change in adaptation to the creature's habits which may be going on in organs which are actively employed.

THE HOMOLOGIES OF THE TEETH.

A superficial survey of the teeth of those mammals which possess two sets of teeth (diphyodonts) will indicate that, notwithstanding the apparent anomalies brought about by adaptive modifications, a close correspondence between the several teeth of different animals exists. That is to say, we can generally identify incisors, premolars, and molars; nay, more, when an animal has less than the full typical number of a particular class of teeth, we can ordinarily say with certainty which of them it is that are absent.

As it is impossible, or at least inconvenient, to avoid the use of the term "typical" dentition, it will be well to explain at the outset what is, and what is not, meant by it.

That the great majority of biologists reject utterly the "archetype" theory, by which all those resemblances which really exist were referred to the influence of a sort of generalised "pattern" animal, according to the model of which all other animals were fashioned, has already been mentioned: this, then, is what is not meant by a "typical" dentition. What is meant, is a form so simplified, so little modified in any special direction, that we can conceive it to be near to a common parent form whence, by progressive modification in

successive generations, other forms have been derived. We cannot point to any mammalian dentition at present known to us, and say this may have been the parent; this is a typical form of mammalian dentition; but we do know many fossil forms which approximate to it more closely than do any at present in existence, and as transitional forms of animals, and animals of highly generalised characters, are every day coming to light, we do not doubt that such forms once did actually exist, and may one of these days be found. But it would probably be as far back as Palæozoic times, whereas our oldest mammalian fossils are Mesozoic.[1] Absolute proof would be obtainable only if we could refer to its place every mammal that had ever existed, and show every step in the series of modifications by which the ultimate divergence of dentition was effected. But evidence far short of absolute demonstration serves to satisfy us on most points, and there is sufficient evidence available to enable us to say with some confidence that our "typical" or parent mammalian dentition was, so far as the numbers of the several kinds of teeth go,

$$i\,\frac{3}{3}\;c\,\frac{1}{1}\;prm\,\frac{4}{4}\;m\,\frac{3}{3} = 44.$$

And when there are less than forty-four teeth, as has been already mentioned, we can in most cases say which they are that are absent.

Thus, taking a certain bear and a baboon (each having two premolars only on each side), we are able to decide, by comparison with allied creatures, that, in the case of the bear, it is the second and third premolars which are wanting, the first and fourth remaining; while in the baboon it is the first and second which are wanting, the third and fourth being present. By homology we mean such correspondence as is above indicated; a correspondence which might almost be expressed as a relationship by descent, in the individual teeth.

(1) But since writing the above, Prof. Marsh has announced the discovery of numerous mammalian fossils in Cretaceous formations.

Homology, then, is almost equivalent to identity of origin, or, at all events, to similarity of origin; but it by no means necessarily involves identity or even similarity in the purpose to which a thing is ultimately applied—a fact which will be further illustrated in speaking of canine teeth.

The homologies of the teeth may be treated under two heads: the one, the homologies of the teeth in their relation to other parts of the body, and the other, their more especial homologies, or their relation to one another.

The relation of the teeth to the skin, which we express by calling them "dermal appendages," as well as the epidermic nature of the enamel, and the dermic nature of the dentine have been sufficiently discussed at former pages, so that we may at once pass to the homologies of the teeth with one another.

Teeth are divided into incisors, canines, premolars, and molars, but these classes do not all admit of quite satisfactory definition. Incisors are defined as teeth implanted in the intermaxillary bone, a definition which has the merit of being precise; and on the whole there is a certain resemblance running through incisor teeth in most animals, but the definition of lower incisors as being the corresponding teeth in the lower jaw is a good deal less satisfactory, because they are not situate upon any distinct bone. And it has even been denied that there can be a true homology between a maxillary and a mandibular tooth.

Molars are teeth at the back of the mouth, which come up behind the milk teeth (when there are any), and which are generally subservient to grinding the food.

Premolars are teeth in front of the molars, usually differing from them by being more simple in form and being smaller, and, in most animals, by having displaced deciduous predecessors. But they are not always simpler in form, nor smaller (*e.g.*, in the horse), nor do they always displace deciduous predecessors (*e.g.*, they do not all do so

in the Marsupials), so that this definition is not absolutely precise. Still, as a matter of practice, it is usually easy to distinguish the premolars, and the division into premolars and molars is useful.

Any objection that can be raised to the name of premolar on the score of a short logical definition being impossible, applies with tenfold force to the canines. (Cf. Messrs. Moseley and Lankester, Journ. Anat. and Physiology, 1869.)

The nearest approach to a good definition is that which describes the canine as the next tooth behind the intermaxillary suture, provided it be not far behind it; and the lower canine as the tooth which closes in front of the upper canine.

A great deal of confusion has arisen out of the twofold sense in which the word "canine" is used: if it were always applied to designate the first tooth in the maxilla of the typical mammalian dentition quite irrespective of its size, &c., and the lower tooth closing in front of it, no objection to its employment could be made, inasmuch as it would designate truly homologous organs.

But it so happens that the tooth in question is, in a very large number of familiar animals, developed to a large size and sharply pointed for use as a weapon, and so with the word canine there comes to be associated a teleological idea; and hence we are dissatisfied with calling the first maxillary tooth "canine," when there is some other tooth which is doing its work.

On the other hand, if we are to leave out of court all considerations as to size, purpose to which it is to be applied, and so forth, there is nothing left to make it deserving of a name distinguishing it from the four teeth behind it. So we must be content with some such statement as the following.

A very large number of animals, notably the Carnivora, have one tooth, situated a little way from the front of the

mouth, developed to an unusual length and sharply pointed, for use as a weapon. The tooth which has undergone this adaptive modification is usually the first which lies in the maxillary bone; in fact, the foremost of the premolar series; but it occasionally happens that it is some other tooth which has undergone this modification. When we use the term canine we should generally mean a tooth so modified, and generally, but not always, should be alluding to the same tooth, *i.e.*, to the tooth which in the typical mammalian dentition comes next behind the outermost incisor—the first of the premolars, if we allow five premolars instead of four.

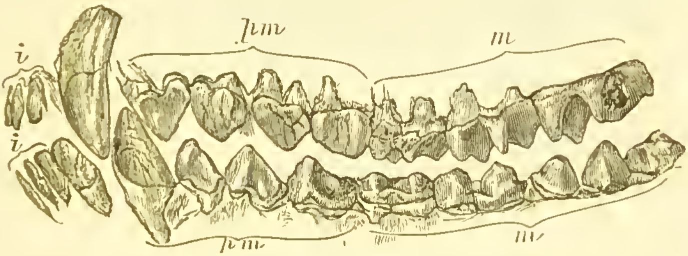
It would practically be very inconvenient to abolish the term canine; but it should be borne in mind that its significance is merely equivalent to "caniniform premolar," and that in describing the dog's dentition (p. 328) we should be less liable to be misinterpreted, were we to say that it has five premolars, of which the first is caniniform. To those who accept the doctrine of evolution it is not needful to say more, as it is hardly possible to resist the conclusion that the teeth of the parent forms were, like those of the present monophyodonts, not much differentiated from one another. Then, as animals diverged and became modified in accordance with their requirements, their teeth would become so far differentiated that they would admit of being classified. Thus the Carnivora would have attained to a stage of differentiation in which the canine is functionally certainly deserving of a distinction, whereas along other lines of descent, differentiation having not proceeded so far, or having proceeded in a somewhat different direction, it would not merit a distinctive appellation.

But it will be desirable to point out a few instances of the difficulties to which those anatomists are committed who call some tooth a "canine" in every case where a tooth is situated in the maxillary bone, close behind the suture

which connects it with the intermaxillary bone, whether that or any other tooth be large and pointed, "caniniform" or not.

In typical Ruminants, the upper jaw lacks both incisors and canines (with certain exceptions, for which see p. 299), but in front of the lower jaw there are grouped together eight teeth, closely fitted together, and of almost exactly similar size and shape. The outermost pair of these teeth are called canines, because (i.) in some allied species the tooth

Fig. 126 ([1]).



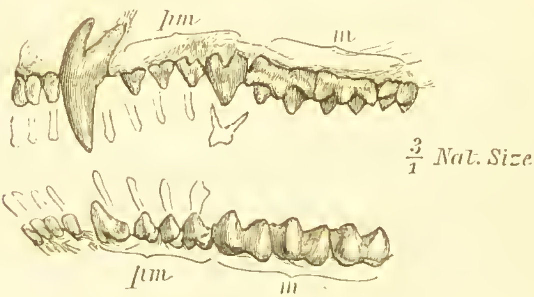
in this situation is more pointed; (ii.) because this tooth shuts in advance of the upper canine when the mouth is closed (in those allied creatures which have an undoubted upper canine); (iii.) because it is cut later than the others (Owen).

These three reasons are weak, because (i.) form is a very unsafe guide to homology, and as to the lateness of its development (iii.), it succeeds to the third incisor, by Professor Owen's own showing, after about the same lapse of time which separated the eruption of the second and third incisors. Moreover, Oreodon, an extinct Ruminant with

([1]) Oreodon Culbertsonii (after Leidy). It will be observed that in the upper jaw the four premolars of the typical mammalian dentition are behind the "canine," but that in the lower jaw the tooth which would fulfil the functions of a canine is the first of these four, and therefore is not the corresponding tooth to the "canine" in the upper jaw.

caniniform teeth, has the eight incisors in the lower jaw in *addition to a caniniform tooth, which is the fifth tooth counting from the front.* With reference to the relative positions of the upper and lower teeth, determining which is and which is not "the canine," (ii.) no one, looking at the dentition of Oreodon, would be inclined to hesitate which teeth he should call "canines;" yet the lower caniniform tooth

FIG. 127 (1).



shuts behind the upper, and therefore, according to this test, it is not a true canine.

In the Lemurs there are similarly eight procumbent teeth occupying the front of the lower jaw, of which the outermost pair are called canines, although not in the smallest degree meriting that name for any other reason than that they close in front of the caniniform tooth of the upper jaw, for they are just like the other incisors.

But it is in the *Insectivora*, which in some respects represent an ancient and generalised mammalian form, that the greatest difficulties occur.

To the mole no less than four dental formulæ have been assigned, all turning upon the identification of the canine.

(1) Upper and lower teeth of the common mole. In it, just as in Oreodon, the teeth which fulfil the functions of canines are not corresponding teeth in the upper and lower jaws.

The difficulty is this: The upper tooth, which looks like a canine, has two roots, and is implanted (and its deciduous predecessors also lie: Spence Bate) within the limits of the premaxillary bone. And besides this, the lower tooth, which answers the purpose of, and looks like, a canine, closes behind instead of in front of the great upper tooth.

Ericulus has a sharp, long, two-fanged tooth, in pattern of crown an enlarged premolar, in position of upper canine, and no caniniform tooth in lower jaw.

Centetes has typical canines, like a Carnivore.

Hemicentetes. The so-called canine, differs in no respect from the premolars behind it.

Erinaceus. So-called upper canine, two-rooted, and like the premolars which follow behind it.

Gymnura. Upper canine-like tooth has two roots; a single-rooted lower pointed tooth closes in front of it.

Macroscelis and *Petrodromus*. The third or outermost incisor is two-rooted, long, and sharp, and plays the part of a canine.

Potamogale. A small tooth, in no respect different from the other premolars, is called a "canine."

In some of the groups no tooth has been lengthened and pointed, so as to serve as a canine; in others it is the wrong tooth, *i.e.*, not the same tooth as in the Carnivora, or as in other Insectivora. Consequently, in the Insectivora the elevation of a tooth into caniniform length and character is a mere adaptive modification, which may affect an incisor, or a premolar, or no tooth at all.

A large number of the small Mesozoic mammals had two-rooted canine teeth (Marsh).

It appears to me that the result of all investigations into the homologies of mammalian teeth may be summed up somewhat in the following manner.

The evidence of a common pattern, which is traceable in incisors, canines, premolars, and molars, would seem to indicate that their special forms have been all derived from modifications of some much more simple form, and that if we are ever to find what might be called a parent

mammalian dentition, it will be nearly "homodont:" that is to say, the several teeth will not differ much from one another in size and shape, just as we see to be the case in the dolphin or the armadillo.

If we were able to place in unbroken series all the dentitions through which, by progressive modification, the original almost homodont dentition had passed into a highly specialised dentition, like that, say, of the cat, it would be a matter of impossibility to fix upon any point where we should be justified in asserting that here the homodont dentition has recently become heterodont: at this point, for the first time, we have incisors, canines, molars.

The earliest mammalian dentitions known to us carry us back no further than Mesozoic times,[1] and of the Mesozoic mammals we may say that they had mostly smooth cerebral hemispheres, no inflection of the angle of the lower jaw, and forty-four or more teeth: of these the canines had two roots and the premolars and molars were little differentiated from one another. The generalised members of these, whom Prof. Marsh proposes to group under the new order Pantotheria, were perhaps the ancestors of the modern specialised Insectivora (American Journal of Science, April, 1887).

The usual pattern of tooth was tricuspid, the central cusp greatly preponderating, but it remains uncertain whether these Mesozoic mammals were Marsupials or Placentals, or whether they may be generalised forms from which both have been subsequently derived.

The Amphitherium (lower jaw alone) is one of the earliest dentitions known, coming from the Jurassic formations; it had sixteen teeth, which, so far as their forms can tell us, were

$$i\,\frac{\quad}{3}\quad c\,\frac{\quad}{1}\quad pm\,\frac{\quad}{6}\quad m\,\frac{\quad}{6}$$

But from the Purbeck bone bed quite a number of forms

([1]) See footnote on p. 305.

have been described, some of which have several incisors, and a general insectivorous type of dentition (Polyprotodonts); others have a single long-pointed incisor on each side of the median line (Diprotodonts) like existing kangaroos, and compressed blade-shaped premolars, so that even at this period much differentiation had already taken place, and we are far from generalised parent forms.

It is noted by O. Schmidt that specialisation of teeth often goes hand in hand with specialisation of the extremities.

A large number of extinct Ungulata had the full typical number of mammalian teeth, viz., forty-four, and in some the individual teeth, incisors, canines, premolars, and molars, passed into one another by insensible gradations, and contiguous teeth were but little differentiated from one another. Professor Flower has described and figured such an extinct Ungulate under the name of Homalodontotherium (Philos. Trans. 1874). It is exceedingly interesting to find that far back in geological time the dentitions were more generalised, both carnivorous and herbivorous mammals of the Eocene period usually possessing the full typical number of teeth, and displaying less of special modification; but the few forms of life which have been handed down in a fossil state do not as yet offer us by any means an unbroken chain of forms differing from one another by progressive modification, except in a few cases: thus the ancestry of the horse is now comparatively completely known to us.

Bearing in mind that the several kinds of teeth have probably a common origin, the homological differentiation in the incisors, premolars, and molars may be advantageously admitted, and made use of as a basis for comparing and classifying the teeth of different animals. It is usually said that when incisors are missing from the full typical number, they are lost from the outer end of the series: that is to say, if there is but one incisor it is I_1; if two, I_1 and I_2.

There are many exceptions to this: *e.g.*, the first incisor

is the first to disappear in the otter, walrus, and some few others, and a question has been raised as to the homologies of man's two incisors.

When premolars are missing, it is said that they are lost from the front of the series. This is generally true, but there are many exceptions, of which the following may be given.

In many bears the second premolar is often lost, as is also the third, but the first and the fourth are very constant; this is also true of some bats. ([1])

To make this more clear, Mr. Oldfield Thomas proposes to write out in full the dentition, thus :—

Bear :—

$$i\,\frac{1.2.3}{1.2.3}\;c\,\frac{1}{1}\;pm\,\frac{1.0.0.4}{1.0.0.4}\;m\,\frac{1.2.0}{1.2.3}$$

There seems good reason to suppose that although modern marsupials have but three premolars, the original number was four, as in placental mammals; and among the Dasyuridæ, a study of the genus Phascologale, in which pm_2 and pm_3 are very constant, but pm_4 variable down to being a minute and functionless tooth in one species, has shown that in Dasyurus, with its two premolars, it is pm_4 that has gone for one.

And a comparison of many specimens, in one of which (Phascologale) four premolars were present, pm_2 being smaller than the others, and a skull of Dasyurus in which a rudimentary tooth was present between its two premolars, indicates that the other which has disappeared was pm_2.

$$\text{Thus Dasyurus has pm}\,\frac{1.0.3.0}{1.0.3.0},$$

$$\text{and Thylacinus pm}\,\frac{1.0.3.4}{1.0.3.4}.$$

([1]) This is ascertained by the examination of allied forms, in which the third premolar is found to be so small as to be rudimentary.

A difficulty at times occurs in deciding whether a tooth is to be regarded as a premolar, or as a milk tooth, as there are many so-called permanent teeth which are lost early in the lifetime of the animal.

Professor Flower gives an instance of this in the hippopotamus: the first premolar appears with the milk teeth; it probably had no predecessor, and is shed in middle life. But in allied forms the corresponding tooth remains in place throughout the creature's life.

The wart-hog is a conspicuous example of the early loss of teeth which clearly belong to the permanent series, all the teeth, (premolar and molar) in front of the last great molar being cast off, and the dentition ultimately reduced to—

$$i\ \frac{2}{3}\ c\ \frac{1}{1}\ m\ \frac{1}{1}$$

That general correspondence which is found to exist between the dentitions of various animals, extends also to the patterns of individual teeth, so that we are able to trace out the various stages by which complexity of pattern has been arrived at.

In what might be termed a typical tooth we should have a single central pulp cavity surrounded by a body of hard dentine; over the crown this is coated by enamel, whilst the whole, crown and root, would be invested by a layer of cement.

The layer of coronal cement may be so thin as to be merely rudimentary, as in Man or the Carnivora; or the investment with enamel may be only partial, as upon the front of a Rodent incisor; or a tooth may be composed solely of a mass of hard unvascular dentine, as in the teeth of the Wrasses.

And just as endless varieties of teeth may be produced by the suppression, or partial suppression, of certain of the tissues, so differences may be brought about by the occur-

rence of other than the three usual tissues. Thus the remains of the central pulp cavity often becomes occupied by calcified pulp, forming "osteodentine;" this, which occurs in man as an almost pathological condition, is perfectly normal in many animals; in the sperm whale, for instance, or in the constantly growing teeth of the sloth, the central axes of which are occupied by dentine permeated by medullary canals.

It is not so much the complexities induced by variation in minute structure that concern us here, as those brought about by the arrangement of the different tissues.

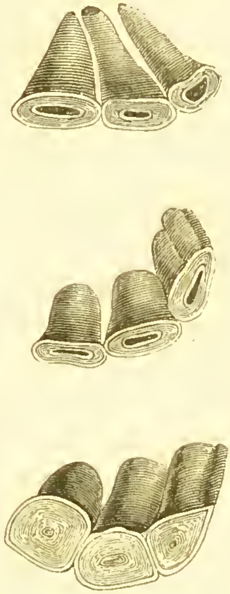
If we take a simple conical tooth with one cusp, such as a canine, and grind or wear down its apex till the terminal portion of enamel is removed, its blunted end will present a more or less circular area of dentine, surrounded by a rim of enamel. If we imagine a tooth with four long similar cusps, we shall at a certain stage of wear have four such areas, while eventually, as the tooth gets worn down below the level of the bases of the cusps, there will come to be a single larger area of dentine surrounded by enamel. Thus in those teeth the grinding surfaces of which are rendered complex in pattern by the presence of several cusps, the pattern changes from time to time as the tooth wears down; while the addition of thick cementum filling up the interspaces of the cusps, adds a further element of complexity, as is seen in the teeth of most herbivorous creatures. The change of pattern induced by the wearing down of the surface to a lower level is well and simply illustrated by the "mark" of the incisor teeth of a horse.

In an uncut, and therefore perfectly unworn tooth, the condition of the apex may be compared to the finger of a glove, the tip of which has been pushed in or invaginated. The depression so formed is, like the rest of the surface, coated with enamel, and with a thin layer of cementum.

When the tooth is worn down to a considerable extent, we have a field of dentine, in the centre of which is an oval ring of enamel; within this a space filled with the débris of food, &c. This constitutes the mark, and as the

Fig. 128 (1).

Fig. 129 (2).



tooth becomes further worn down, below the level of the bottom of the pit, the mark disappears, and a plain area of dentine results.

Interesting as have been the discoveries made of late years in mammalian palæontology, it is not as yet by any means possible to say that all complex mammalian teeth may be considered to have been derived from a simple conical tooth; though the pattern of some, for example, of the molars of the horse, may be traced back in increasing simplicity through a number of parent forms.

Virchow, in relating a case in which the place of an upper

(1) Horse incisor, in longitudinal section.

(2) Horse's incisors, showing the mark at various ages.

molar had been taken by three peg-shaped denticles with separate roots, suggests that this may have been due to atavism, and that multicuspid teeth may have been formed by the coalescence of several separate teeth of the homodont parent dentition. But a study of the evolution of complex forms of tooth crown from simple ones seems to negative this hypothesis. And Dr. H. F. Osborn (American Naturalist, Dec. 1888) has made an important contribution to this subject by wide-spread investigations, the result of which is to indicate that a tritubercular molar was almost as universal among Mesozoic mammals as a pentadactyle foot. The three cusps were arranged in a triangle, the single cusp lying to the inner side (antero-internal) in the upper, and to the outer in the lower molars; and the whole triangle of cusps of the lower tooth passed in front of that of the upper in closure of the mouth, the teeth of the two jaws thus alternating rather than meeting grinding surface to grinding surface. He believes that these "three primary" cusps "formed a central stage from which the great majority of recent molar types have diverged by the addition, modification, and reduction of cusps: we must except the Monotremes, the Edentates, and possibly the Cetaceans, although there is considerable evidence that the Cetacean molars were once of the Triconodont type."

Believing that a simple cone was the original form, a tritubercular form had been reached by the Mesozoic period, and these three primary cusps may be traced and their homologies established in later and more complex molar patterns; the added or secondary cusps following certain lines and allowing of the establishment of their homologies, though with less certainty.

It is very interesting to note that even when teeth have become flat-topped and quadri or quinque-tubercular, the primary triangles of the upper and lower teeth retain their old relative position, *i.e.* alternate with one another.

Dr. Osborn proposes a nomenclature[1] for the cusps, slightly less cumbrous than "antero-external," &c., &c., but whether it will obtain currency time must show: he gives names to six cusps on both upper and lower teeth, *i.e.*, to three supplementary ones besides the primary ones.

A very instructive series of comparisons of the molar teeth of Insectivora has been made by Mr. Mivart (Journal of Anat. and Physiol., 1868), pointing out that within the limits of this group a great variety of patterns is met with, the several modifications being connected by transitional forms.

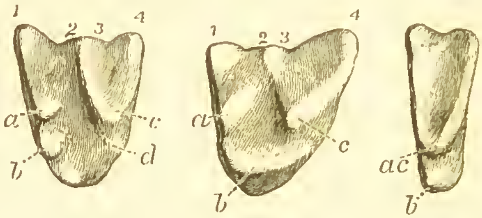
It would appear that upon the molar teeth (upper) of Insectivora there are four principal cusps (lettered a, b, c, d, in the figure) which are more or less connected by ridges; such simple teeth are met with in the elephant mice (Macroscelides) and hedgehog. The cingulum is well developed in most of the group, and the further complexity of the crowns, which often bristle with sharp points, is brought about by the elevation of the cingulum into long sharp points, equalling, or exceeding in length, the principal cusps of the tooth.

Thus in Urotrichus, a Japanese creature having affinities with the mole, the external cingulum is elevated into three distinct pointed cusps, united by ridges with the two principal cusps, an arrangement which gives a sort of W pattern to the surface, while to the inner side the cingulum forms another cusp, so that there are in all eight cusps; the common mole has the third cusp developed from the outer cingulum, but its two inner principal cusps are fused together

[1] Protocone = Antero-internal cusp of upper molar; ? homologue of the single cusp of primitive tooth.
Paracone = Antero-external cusp of upper molar.
Metacone = Postero-external cusp of upper molar.
Protoconid = Antero-external cusp of lower molar.
Paraconid, metaconid = corresponding cusps of lower teeth.

and lose their distinctiveness. The suppression and fusion of cusps is carried to a much greater extent in the compressed teeth of the iridescent mole (Chrysochloris), but there are intermediate forms which render it easy to identify its reduced parts with those corresponding to them in the mole or in Urotrichus.

Fig. 130 (1).



Speaking generally, it may be said that new cusps are added to the number already existing, by the cingulum becoming elevated into points ; it is not very unusual to see subsidiary cusps obviously originating in this way upon human molars.

Ridges may variously connect the cusps ; and the coalescence of two or more cusps to form an exceedingly elevated point is illustrated by the carnassial tooth of Carnivora ; to this transformation certain marsupial teeth form the clue, as they afford unquestionable evidence of such coalescence by a gradational series of small modifications in this direction occurring in allied creatures.

A common pattern of tooth is formed by the junction of the two anterior and two posterior cusps by simple ridges ;

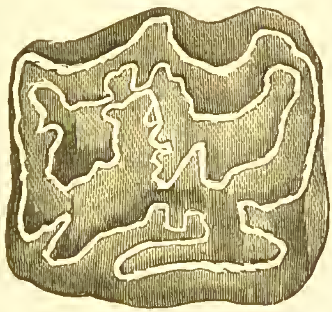
(1) Upper molar teeth of (A) Urotrichus ; (B) Mole ; and (C) Chrysochloris. The four principal cusps are lettered *a*, *b*, *c*, *d*, in each of the figures. In A the cingulum has been elevated so as to form four additional cusps on the exterior of the tooth, and one additional cusp on the interior. B and C show the fusion of certain of these cusps, and the consequent diminution in their number. (From Mivart.)

and the cingulum may connect the outer ends of these two ridges; such a tooth is seen in the Tapir, and in the Palæotherium. By the varied obliquity of these ridges, and by the introduction of secondary inflections, patterns apparently dissimilar are arrived at.

In the molar tooth of the horse, arrived at by a modification of the Palæotherium type, we have a surface constantly kept rough by the varying hardness of its different constituents.

In a worn tooth, we have upon a general field of dentine two islands of cementum, bounded by tortuous lines of enamel, and on the inner side a sort of promontory of

Fig. 131 (1).



dentine, bounded by enamel. The tortuous lines of enamel by virtue of their hardness will, at all stages of wear, be more prominent than the dentine or the cementum, and will hence maintain the efficiency of teeth as grinders.

The patterns of grinding surface thus produced, are very constant for allied species, so that an individual tooth of a herbivore may sometimes be correctly referred to its genus, and always to its family.

But as it will be necessary to recur to this subject from time to time, it will suffice for the present to point out that

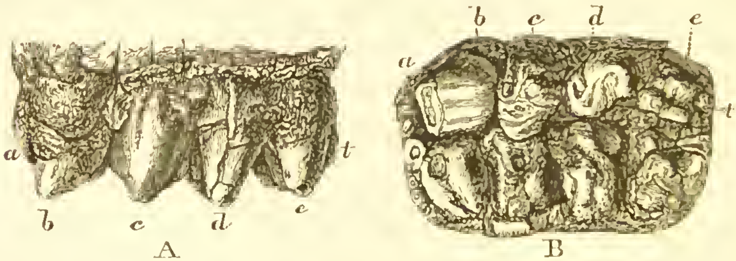
(1) Molar tooth of Horse, showing the characteristic pattern of its grinding surface.

such correspondences do exist, and that all the complexities of pattern found, may, in practice, be reduced to some few types.

The development of additional cusps from up-growths of the cingulum, and the suppression or fusion of pre-existing cusps, may be traced by a comparison of the teeth of allied animals, and thus connecting links are found between patterns at first sight very dissimilar. The order Proboscidea affords, however, so instructive an instance of the manner in which an exceedingly complex tooth has been derived from a simple one, that it may be mentioned in this place as an example.

The tooth of the elephant is so strikingly unlike other teeth that it might at first sight be supposed that it is

Fig. 132 [1].



more essentially different than is really the case. The clue to its nature is afforded by the teeth of an extinct Proboscidian, the Mastodon. If we take as our starting point the second true molar of one of the Mastodons (Tetralophodon) we find its crown to be made up of four strongly

(1) Second upper molar of Mastodon (longirostris), from Falconer. About one-eighth natural size. The four transverse ridges, *b*, *c*, *d*, *e*, are seen to be, to some extent, divided into outer and inner divisions by a longitudinal cleft, much less deep than the transverse indentation. At the front there is a slight elevation of cingulum into a "talon" (*a*), and a similar one at the back of the teeth; by its further elevation additional ridges or cusps would be formed.

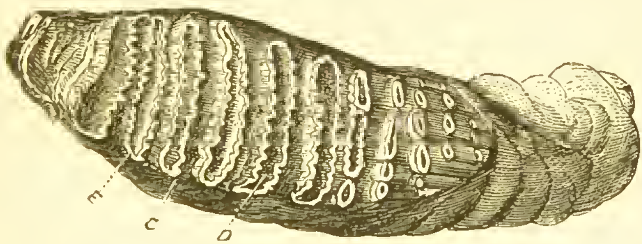
pronounced transverse ridges, the summits of which are made up of rounded eminences (whence the name Mastodon, from μαστος, a nipple). The three transverse ridges coalesce at their bases, and the crown is supported upon a number of roots corresponding to the ridges.

If we take the next tooth, or the third true molar, the general character remains the same, save that there are five ridges, and indications of as many roots ; still the general correspondence of the ridges with the cusps of less aberrant teeth is obvious.

The crown is coated by enamel, over which there is a thin layer of cement, which does not fill up the whole interval between the ridges.

Thus the tooth is not a very aberrant one ; it is obviously nothing more than a tooth in which the somewhat numerous

FIG. 133 ([1]).



cusps are connected by transverse ridges, and are very long and strongly pronounced.

To convert the tooth of a mastodon into that of an elephant, we should have to multiply the number of ridges, to further increase their depth, to fill up solidly the interspaces between them with cementum, and to stunt the roots. The completed tooth of an elephant is a squarish or rather oblong mass, from the base of which spring contracted and stunted roots. It consists of a common pulp

([1]) Molar Tooth of an Asiatic Elephant, showing the transverse plates of dentine bordered by enamel.

cavity, small in proportion to the bulk of the tooth, and deep down in the mass; from it many thin laminæ are sent up towards the surface, each forming the core of an area of dentine enclosed by enamel; and the interspaces of these exaggerated cusps are solidly filled in by cementum.

Between the Mastodon and the Indian Elephant are a number of transitional forms in which we are able to trace the gradual modification of the not excessively aberrant tooth of the Mastodon into the very peculiar huge molar of the Indian Elephant.

The numerous transverse plate of the elephant's grinders are united by dentine at their bases, and a common pulp cavity and truncated roots are formed; but in this last

FIG. 134 [1].

Nat. Size

respect the molar teeth of the Capybara depart still farther from the ordinary type, for being molars of persistent growth, their numerous transverse plates of dentine and enamel do not become continuous, and there is no common pulp cavity. It is as though in an elephant's grinder the plates, which are for a long time distinct, never coalesced, but continued to grow on separately, being united with their fellows by cementum only.

It has been suggested (J. A. Ryder, Proc. Acad. Nat. Sciences, Philadelphia, 1878), that the pattern of the molar teeth of herbivora is the result of the extent and direction of the excursions of the mandible when it is in use, and so depends upon the form of the glenoid cavity and of the

[1] Molar of Capybara, showing the transverse plates of dentine and enamel united to one another by cementum.

condyle, and that hence the greatest modification is to be found nearest to the articulation, where the greatest force is exerted.

Thus "bunodont" animals, *i.e.* those that have rounded conical cusps upon their short-rooted teeth, have a cylindrical condyle; selenodonts, or those with crescentic ridges on the molars, have a condyle which is expanded and plane, while lophodonts, or those with transversely ridged teeth, have a globular condyle.

That there is some correspondence between the condyle, the movement of the jaw, and the form of the teeth is a fact, but it is not so easy to see how it is brought about.

The simple mechanical explanation that the teeth are so to speak drawn out into these forms, whether in one or in ten thousand generations, does not commend itself to my mind. For that portion of the tooth which is subject to these direct influences is hard and rigid, and its form, whatever it be, is unalterable: in order to alter the form of a masticating surface by direct mechanical means, the influence would have to be brought to bear upon the teeth while they are yet soft, when they are still buried within the jaw.

And it is believed by many evolutionists that acquired properties, *i.e.*, those acquired by the individual under outside influences after its birth, are never inherited, but that nothing is inherited save variations, the capacity for which pre-existed in the ovum and the sperm cell.

Without going the length of altogether subscribing to this doctrine, the difficulty of seeing how a mechanically-acquired character should be inherited, is at least as great as the difficulty of realising how advantageous specialisations should be carried further and intensified by the ordinary laws of natural selection.

THE MILK DENTITION.

Some thirty years ago Professor Owen called attention to the fact that those mammals in whom the teeth situated in different parts of the mouth were alike in form (homodonts), developed only one set of teeth, and to indicate this characteristic he proposed for them the term "monophyodonts." Those, which, on the contrary, had teeth of different size and form in various parts of the mouth (heterodonts), developed two sets of teeth; a "milk" set, which was displaced by a permanent set, and this peculiarity he expressed by the term "diphyodonts." As originally set forth, the terms homodont and monophyodont were interchangeable, for they designated the same groups of animals; in the same way heterodont was an equivalent for diphyodont.

But although this is true of a large number of animals, it is not true of all, and it becomes necessary to note some of the exceptions.

The nine-banded armadillo (Tatusia peba) is a true homodont: its teeth are all very nearly alike, they are simple in form, and they grow from persistent pulps. Yet it has been shown by Rapp, Gervais, and Professor Flower, to have a well developed set of milk teeth, retained until the animal is of nearly full size.

Thus it is a true diphyodont, at the same time that it is a true homodont mammal. But no milk dentition has been observed in the sloths, nor indeed at present has it been seen in any other armadillo (except the doubtfully distinct T. Klapperi); nor have milk teeth been found in any Cetacean, so that the rest of the homodont animals are, so far as we know, really monophyodont.

Nor is it absolutely true that monophyodonts are all homodont: thus the rudimentary teeth of Balænoptera are heterodont (see p. 342).

Upon the whole, our information respecting the "milk"

or deciduous dentition is defective; but much light has been thrown upon the subject by the investigations of Professor Flower (Journal of Anatomy and Physiology, 1869, and Transactions Odontological Society, 1871), of whose papers I have made free use in this chapter.

The perpetual replacement of teeth lost, or shed in regular course, which characterises the dentition of fish and reptiles, finds no parallel in the case of mammals, none of whom develop more than two sets of teeth.

Just as homodont mammals as a rule develop but one set of teeth, so heterodont mammals as a rule develop two sets of teeth, though exceptions to this rule may be found.

The deciduous or milk set of teeth may be of any degree of completeness; the milk teeth in man answer the requirements of the child up to the age of seven years, and in the Ungulata they commonly remain until the animal has assumed its adult proportions. On the other hand, in many "diphyodont" animals the milk teeth disappear very early indeed, as in the mole (see page 310); whilst there are many instances of the milk teeth being absorbed in utero. So that in the extent to which the milk teeth are developed, the greatest variability is found to exist.

A perfectly typical milk dentition represents, upon a reduced scale, the adult dentition of the animal, with the exception only that sexual differences are but feebly marked, if indeed they are at all present.

Thus, as a general rule, the hindmost of the milk teeth bear more resemblance to the true molars which come up behind them, than they do to the premolars which come up from below to displace them, which latter are generally of simpler form.

In what may be termed the normal arrangement, each tooth of the milk series is vertically displaced by a tooth of the permanent series; but plenty of examples may be found of particular milk teeth which have no successors,

and, on the contrary, of individual permanent teeth which have never had a deciduous predecessor.

It has already been mentioned that amongst homodonts no succession of teeth has been observed in the Cetacea,

FIG. 135 (1).

FIG. 136 (2).

nor in any other of the Edentata, save the armadillo; amongst heterodonts there are several Rodents which have no deciduous teeth, *e.g.*, the rat; the dugong has probably deciduous incisors, but no other milk teeth; the elephant has no vertical succession, save in the incisors.

Among Marsupials, which are true heterodonts, there is only one milk molar on each side in each jaw; this is always

(1) Permanent and milk dentitions of a Dog; the latter was well developed. Nat. size.

(2) Permanent and milk dentition of a seal (Phoca Greenlandia). Nat. size.

displaced by the third or last premolar[1]; but the milk tooth varies in the extent to which it is developed from being rudimentary in Thylacinus, probably absent altogether

Fig. 137 (2).

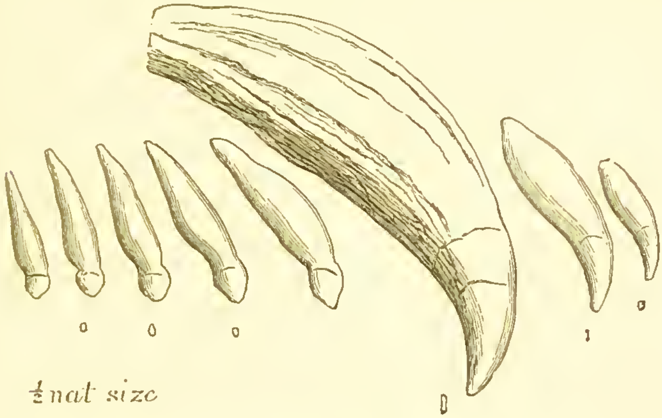
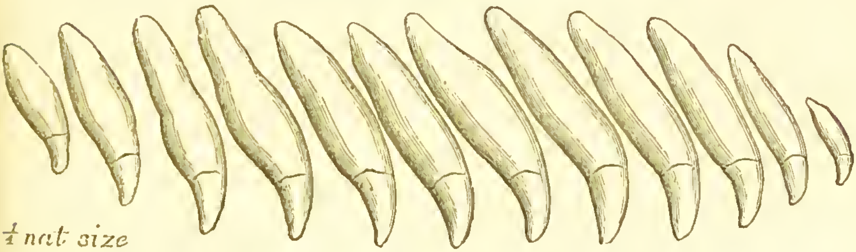


Fig. 138 (3).



in Dasyurus,[4] and Phascolarctus, to being a large tooth retained in full use till the animal is nearly full grown in Hypsiprymnus.

Within the group Carnivora, the dog and many others have a thoroughly well developed set of milk teeth, which

(1) Probably this is really pm_4.

(2) Permanent and milk dentition of an Elephant Seal (Cystophora proboscidea).

(3) Teeth of the truly monophyodont Grampus (Orca capensis). (These four figures are copied from Prof. Flower's paper).

(4) See, for a more detailed account of the milk dentition of Marsupials, the chapter relating to them.

do service for some time; in the bear the milk teeth are relatively smaller, and are shed very early; in the seal the milk teeth are rudimentary, functionless, and are absorbed before birth, so that in the specimen figured the milk incisors had already disappeared (see Fig. 136).

In the elephant seal the milk teeth are yet more rudimentary, and the difference between its dentition and that of the monophyodont homodont cetacean (Grampus) is not great; an observation which is the more interesting, inasmuch as this seal in other characters than its teeth approaches towards the cetacean group. From these facts, which are well indicated in the accompanying figures, Professor Flower argues that the permanent set of teeth of diphyodonts correspond to the single set of monophyodonts, so that the milk dentition, when it exists at all, is something superadded.

Whether this be so is a question difficult to determine; from the facts advanced by Professor Flower, while they stood alone, most people would, with little hesitation, concur with his conclusion, and this interpretation is endorsed by Mr. Oldfield Thomas, but the history of the development of the teeth interposes a difficulty.

The tooth germ of the milk tooth is first formed, and the tooth germ of the permanent tooth is derived from a portion (the neck of the enamel germ) of the formative organ of the milk tooth (see Fig. 68). Again, in most of those animals in which there is an endless succession of teeth, such as the snake, the newt, or the shark, each successive tooth germ is derived from a similar part of its predecessor, the natural inference from which would be that the permanent set, being derived from the other, was the thing added in the diphyodonts.

The question cannot be finally settled until we know more of the development of the teeth of the monophyodont Cetacea: thus it might turn out that in them also there are abortive

germs of milk teeth formed, which do not go on so far as calcification, but which do bud off, as it were, germs for permanent teeth; if such should prove to be the case, this would bring their teeth into close correspondence with those of the elephant seal.

The investigation of these questions is further complicated by the fact that there are quite numerous instances of "permanent" teeth, that is teeth unquestionably belonging to the second set, which are shed off early, and do not remain in place through the lifetime of the animal; an example of this is to be found in the Wart Hog (Phacochærus), which loses successively all its premolars and the first and second true molars, the last true molar alone being truly persistent.

In the Ornithorhyncus we have an example of the loss of teeth, which doubtless in some ancestral form were both more numerous and more persistent, and the Cyclostomatous fish (see page 228) appear also to be instances of degradation in this respect. So also the seal would appear to be in the state of having really lost its milk dentition : indeed, it is difficult to understand how upon the evolution hypothesis, the earlier stages of the introduction of a milk dentition could be preserved and intensified, for they could have been of no use to their possessors.

It is a possible hypothesis that the normal mammalian condition is Diphyodont, and that the Monophyodonts have arrived at the stage of having wholly lost their milk dentitions, whilst in others it has lingered on, as in Tatusia peba in full strength, or as in the seal, in feeble rudiments.

There is a reason, or some show of a reason, for the succession taking place as far back as the premolars, and the molars being exempt from change, which so far as I know, has not been noticed by any of the many writers upon the subject. In all mammals the whole length of the jaw, at the time of birth and afterwards, is occupied by tooth germs and after-

wards by teeth ; it is well ascertained that the manner of growth in the jaw is by backward elongation, and that that portion which is occupied by the molars actually does not exist at the time of birth. Tooth change might therefore be expected to be limited, as in fact it is, to that portion of the jaws which exists early, while the animal is small ; milk teeth could not exist in the molar region, because during their reign the molar region itself does not exist.

Oscar Schmidt suggests that the origin of milk teeth can be traced back to the shortening of the facial region, which gave no room for the full number of tooth germs to lie side by side : the result of this crowding being that they came to lie one upon the top of another, and the teeth lying nearest to the surface, having to be used first, get developed first.

The milk teeth are thus placed at a disadvantage owing to the hostile position of their successors, and according to this view, the Marsupials and seals would have once possessed, but have now lost their milk teeth.

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CHAPTER IX.

THE TEETH OF EDENTATA, CETACEA, AND SIRENIA.

THE TEETH OF EDENTATA (BRUTA).

Sloths, Armadillos, Ant-eaters.

THE term Edentata was applied to the animals of this order to indicate the absence of incisors (teeth in the inter-maxillary bone): though this is true of most of them, a few have some upper incisors, but the central incisors are in all cases wanting.

Some of them are quite edentulous; this is the case in the Mutica, or South American Ant-eaters (Myrmecophaga and Cyclothurus), in which the excessively elongated jaws cannot be separated to any considerable extent, the mouth being a small slit at the end of the elongated muzzle. Food is taken in by the protrusion of an excessively long, whip-like tongue, which is covered by the viscid secretion of the great sub-maxillary glands, and is wielded with much dexterity. The Manis, or Scaly Ant-eater is also edentulous.

The Edentata belong to the monophyodont or homodont section of Mammalia; but, in some, certain teeth are more largely developed than others, so that we have teeth which might be termed canines; and it has already been mentioned that one armadillo, at all events, is diphyodont.

The teeth are of simple form, and do not in any marked degree differ in the different parts of the mouth, except only by their size (to this the canine-like tooth of the two-toed sloth is an exception). They are all of persistent growth,

and therefore no division of parts into crown, neck, and root is possible: they consist generally of dentine and cement, with sometimes the addition of vaso-dentine, into which latter tissue the central axis of the pulp is converted; while in some members of the order other peculiarities of structure exist: thus in the Orycteropus (Cape Ant-eater), dentine like that of Myliobates is found; and in the Megatherium hard dentine, a peculiar vaso-dentine, and richly vascular cementum co-exist (see Fig. 44).

I am not aware that enamel has been seen upon the teeth of any Edentate animal, but I found some years ago that the tooth germs of the nine-banded armadillo were provided with enamel organs; this, however, proves nothing, for (Philos. Trans., 1876) I believe the presence of enamel organs to be universal and quite independent of any after formation of enamel.

The teeth of the nine-banded armadillo (T. peba), will serve to illustrate the character of the dentition of the class. They are seven in number on each side of the jaw, of roundish form on section, and those of the upper and lower jaws alternate, so that by wear they come to terminate in wedge-shaped grinding surfaces: before they are at all worn they are bilobed, as may be seen in sections of the tooth-germs.

In the accompanying figure the milk teeth are represented, and beneath them their permanent successors: the divaricated bases of the milk teeth are due to the absorption set up by the approach of their successors, and not to the formation of any definite roots. Successional teeth have been detected in this armadillo only (except also in T. kappleri, which is perhaps a mere variety); but material does not exist in our museums which would enable us to positively deny their occurrence in other forms.

Professor Flower has failed to discover any succession of teeth in the sloths, and I have myself, through the kindness of the late Professor Garrod, examined microscopically the jaws

of a fœtal Cholœpus, in which the teeth were but little calcified, and failed to detect any indication of a second set of tooth-germs. The probability is, therefore, that they are truly Monophyodont.

In the armadillos the teeth are always of simple form and about thirty-two in number, except in Priodon, which has as many as a hundred teeth, a number altogether exceptional among mammals.

Sloths have fewer teeth than armadillos, and these softer in character, the axis of vaso-dentine entering more largely into their composition, and forming as much as half the bulk of the tooth.

The two-toed Sloth has $\frac{5}{4}$ teeth in each jaw, and these are

Fig. 139 ([1]).

nearly cylindrical in section and of persistent growth. In the region of the canine tooth is a tooth which is of larger size than the rest.

The Orycteropus, or Cape Ant-eater, the peculiarities of whose teeth have already been alluded to, has about thirty-six teeth in all; but these are not all in place at one time, the smaller anterior teeth being shed before the back teeth are in place.

The true Ant-eaters are all edentulous. The teeth of some of the gigantic extinct Edentates were a little more complex in form and structure; thus the teeth of the Glyptodon were divided by longitudinal grooves, which in

([1]) Lower jaw of a young Armadillo (Tatusia peba), showing the milk-teeth (*a*) in place, and their successors (*b*) beneath them. From a specimen in the Museum of the Royal College of Surgeons (after Flower).

section rendered it trilobed; and the teeth of the Megatherium were likewise marked by a longitudinal furrow.

In their persistent growth, uniformity of shape, and absence from the inter-maxillary bone, they strictly conformed with the teeth of recent Edentata.

THE TEETH OF CETACEA.

This order is divided into two groups, namely the toothed whales or Odontoceti and the whalebone whales or Mysticoceti; these two groups are sharply defined from one another.

No cetacean is known to develop more than one set of teeth, and these, when present in any considerable numbers, closely resemble one another in form.

The teeth, however, of the extinct Zeuglodon and Squalodon which have about 361 teeth are heterodont in character.

They are usually composed of hard dentine, with an investment of cement; after the attainment of the full dimensions of the teeth what remains of the pulp is very commonly converted into secondary dentine; tips, and even entire investments of enamel, are met with in many of the order.

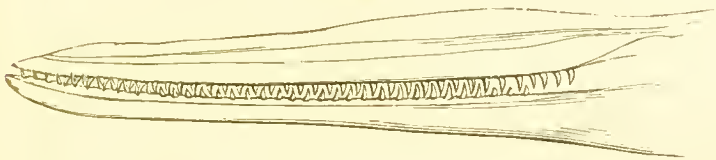
The dentine of many Cetaceans, *e.g.* of the sperm whale, is remarkable for the very numerous interglobular spaces which it contains; these are clustered in concentric rows, so as to give rise to the appearance of contour lines. The cement is often of great thickness, and the lacunæ in it are very abundant; its lamination is also very distinct.

In the dolphin the teeth are very numerous, there being about 200; they are slender, conical, slightly curved inwards, and sharply pointed; as they interdigitate with one another there is very little wear upon the points, which consequently remain quite sharp. The largest teeth are those situated about the middle of the dental series.

Many variations in the number and form of the teeth

are met with; the porpoise has not more than half the number of teeth possessed by the dolphin, while the grampus has still fewer. The teeth of the grampus become worn down on their opposed surfaces, and coincidently

FIG. 140 (1).



with their wearing away the pulps become calcified. In the Oxford museum there is a grampus in which, owing to

FIG. 141 (2).

¼ nat. size

a distortion of the lower jaw, the teeth, instead of interdigitating, became exactly opposed to one another; the consequence of this was that the rate of wear was greatly increased, and the pulp cavities were opened before the obliteration of the pulp by calcification(3), so that the pulps died and abscesses around the teeth had resulted.

In the sperm whale the teeth are numerous in the lower jaw, but in the upper jaw there are only a few curved,

(1) Jaws of a common Dolphin.

(2) Teeth of upper jaw of a Grampus (Orca), (after Professor Flower).

(3) Trans. Odonto. Society, 1873. When I published this paper I was not aware that Eschricht had previously published a similar observation.

stunted teeth, which remain buried in the dense gum. The teeth of the lower jaw are retained in shallow and wide depressions of the bone by a dense ligamentous gum, which, when stripped away, carries the teeth with it. Every intermediate stage between this slight implantation and the well-developed stout sockets of the grampus, is met with in the Cetacea.

In the bottle-nosed whale (Hyperoodon bidens) the only large teeth present are two conical, enamel-tipped teeth (sometimes four) which remain more or less completely embedded within the gum, near to the front of the lower jaw: in addition to these there are 12 or 13 very small rudimentary teeth loose in the gums of both jaws. (Eschricht, Lacépède.)

The Ziphoid cetaceans present one of the most curious and inexplicable dentitions to be found in any animal. The upper jaws are edentulous, as in the Hyperoodon, and the lower jaws contain only a single tooth upon each side; but these teeth have attained to great proportions, measuring in full-grown specimens as much as ten inches in length; they are thin, flat, and strap-shaped, straight for some considerable part of their length, and then curving over towards each other; they even cross each other above the upper jaw so that they actually limit, and that to a very small amount, the extent to which the jaws can be opened.

It is not merely difficult to see what use these teeth can be, but it is hard to suppose that they can be otherwise than actually detrimental to their possessors in the pursuit of food; but there is some reason to suppose that the presence of well developed tusks is a character of the male sex, though upon this point the evidence is not quite complete. Females have been found with their skins curiously scored in two parallel lines, especially near the pudenda, suggesting the idea that they are liable to be attacked by the males.

The structure of these teeth is not less peculiar than their general form; the summit of the tooth, which starts

off nearly at right angles to the shaft (and so, the shaft being curved over the top of the upper jaw, comes to stand nearly vertically) consists of a denticle bluntly pointed, and made up of dentine coated with enamel. This denticle of triangular shape is only about a third of an inch in length, and in the adult specimen described by Professor Sir Wm. Turner had the enamel coat partially worn off.

In the Challenger Reports (Zoology, vol. i.) he says, "In the earlier stage their structure does not differ materially from the ordinary type of tooth one meets with, say in the human or carnivorous jaw, the crown being formed by enamel, the fang by cement, whilst the great body of the tooth consists of dentine, in which is a marked pulp cavity, communicating with the exterior by a slit-like aperture at the root of the fang. The exceptional character these teeth exhibit in the erupted condition is due to the disappearance of the enamel from the crown, to the cessation in the development of the ordinary dentine, to the excessive formation of osteodentine, of modified vasodentine, and of cement, by means of which the pulp cavity becomes almost obliterated, and the fang assumes dimensions which, in the case of Mesoplodon Layardii, lead to the production of a tooth having the very remarkable form and relation to the beak which I have described."

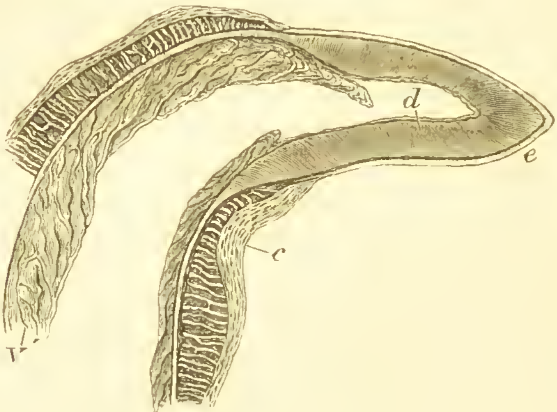
As may be gathered from the above, the development of the tooth starts by the formation of the denticle, which is of an ordinary structure; the enamel however soon ceases to be formed, and but very little further down, so does the true dentine, not however before cementum has begun to be formed upon its exterior (see *c* in fig. on next page). Then there comes an abrupt change in direction, and in the place of true dentine we find a coarser textured tissue which contains large vascular canals.

This Professor Turner and Professor Lankester regard as a vasodentine, seeing that it is in all probability a product

of the dentine pulp. Of this the great mass of the tooth consists, but it has throughout its length an investment of cementum of an ordinary type, which forms a complete exterior layer laminated, full of lacunæ, and for the most part devoid of Haversian canals.

Immediately beneath this layer there is, if the distinction

Fig. 142 ([1]).



be not exaggerated in the drawing, a definite stratum of tissue of material thickness which is characterised by an abundance of vascular canals arranged perpendicularly to the surface (*a* in fig. 142), which is regarded by Professor Turner as belonging to the dentine group of tissue, *i.e.* as being a vasodentine. But there is this difficulty in accepting this view, viz., that near to the denticle it is seen to lie distinctly outside the true fine-tubed dentine (see fig. 142) which it overlaps to a considerable extent; now if this tissue was formed by the dentine pulp we have the anomaly of a pulp first forming a very vascular vasodentine, then changing to forming a fine tubed normal dentine (which is

([1]) Upper part of tooth of Mesoplodon, after Professor Sir W. Turner. *a*, Tissue of doubtful origin, permeated by vascular canals; *c*, cementum; *d*, dentine; *e*, enamel; *v*, vasodentine.

exactly the reverse of what is met with in other creatures in which the pulp forms these two structures), and finally reverting to the building up of a vasodentine.

Judging by analogy this seems so improbable that in the absence of more positive knowledge and simply judging from the figure, I should be inclined to refer this layer to the cementum. Lower down in the shaft of the tooth anastomoses take place between the tubes of this layer and those of the unquestionable pulp products, but anastomoses between dentine tubes and enamel tubes, and between dentine tubes and cement lacunæ are of common occurrence in many animals, so that this communication does not prove anything as to their respective origin.

However Professor Lankester lays stress upon the globular botyroidal structure of this layer, which he states shades off into the fine tubed dentine, so that it may perhaps be regarded as an excessive development of the globular layer of dentine, rather than as a vasodentine. In reconciliation of the discrepancy between the two descriptions, it is suggested by Professor Turner that the vascular canals seen by him in this layer may have become obliterated in the presumably much older specimen described by Professor Lankester.

The central pulp cavity becomes reduced to the merest traces, so that the completed tooth is almost solid.

In the Narwal (Monodon monoceros) two teeth alone persist, and these are in the upper jaw. In the female the dental germs become calcified, and attain to a length of about eight inches, but they remain enclosed within the substance of the bone, and their pulp cavities speedily fill up. In the male, one tusk (in some very rare instances both) continues to grow from a persistent pulp till it attains to a length of ten or twelve feet, and a diameter of three or four inches at its base. This tusk (the left) is quite straight, but is marked by spiral grooves, winding from right to left. It is curious that in one of the speci-

mens, in which the two tusks had attained to equal and considerable length, the spirals on the two wound in the same direction; that is to say, as regards the sides of the head, the spirals were not symmetrical with one another.

The tusk of the male narwal may fairly be assumed to serve as a sexual weapon, but little is known of the habits of the animal.

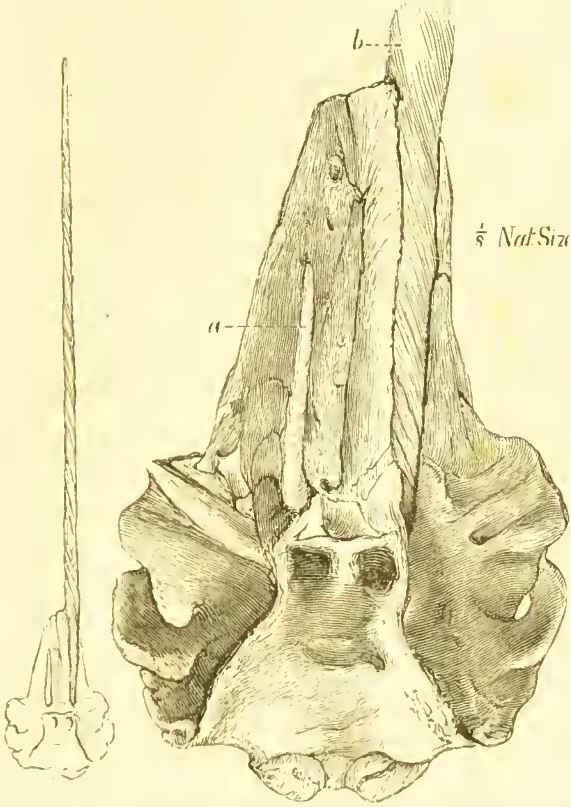
Professor Sir Wm. Turner has lately noted the occurrence of two stunted incisor rudiments in a fœtal narwal: these obviously represent a second pair of incisors, and attain to a length of half an inch, but are irregular in form; they are situated a little behind the pair of teeth which attain to more considerable dimensions. All trace of this second pair of incisors is lost in adult skulls.

The whalebone whales are, in the adult condition, destitute of teeth, but prior to birth the margins of both upper and lower jaws are covered with a series of nearly globular rudimentary teeth, which become calcified, but are speedily shed, or, rather, absorbed.

The fœtal teeth of the Balænoptera rostrata have been carefully described by M. Julin (*Archives de Biologie*, 1880), the *Balænopteridæ* having been previously supposed to be without rudimentary teeth. The ramus contained 41 tooth germs, each furnished with an enamel organ and dentine bulb, with a slight capsule; these were lodged in a continuous groove in the bone above the vessels, thus recalling the condition of the parts in a human embryo at a certain stage. A very small amount of calcification takes place, a mere film of dentine being formed upon the dentine bulb. But what is very remarkable is that the dentine bulbs are simple near the front, bifid in the middle, and trifid at the back of the mouth; in other words, these tooth-germs would go to form heterodont teeth, not unlike those of some seals, or of Squalodon. Hence it has been suggested that the whale may be descended from some such ancestral form.

From the upper jaw of an adult whalebone whale there hang down a series of plates of baleen, placed transversely to the axis of the mouth, but not exactly at right angles to it.

Fig. 143 (1).



The principal plates do not extend across the whole width of the palate, but its median portion is occupied by subsidiary smaller plates. The whalebone plates are frayed out at their edges and collectively form a concave roof to the mouth,

(1) Cranium of Narwal (Monodon monoceros). *a.* Stunted tooth, with its basal pulp-cavity obliterated. *b.* Long tusk. The small figure, giving the whole length of the tusk, shows the proportion which it bears to the rest of the skull.

against which the large tongue fits, so as to sweep from the fringes whatever they may have entangled. The whale in feeding takes in enormous mouthfuls of water containing small marine mollusca, this is strained through the baleen plates, which retain the Pteropods and other small creatures, while the water is expelled. Then the tongue sweeps the entangled food from the fringe of the baleen plates, and it is swallowed. Each plate consists of two dense but rather brittle laminæ, which enclose between them a tissue composed of bodies analogous to coarse hairs. By the process of wear the brittle containing laminæ break away, leaving projecting from the edge the more elastic central tissue in the form of stiff hairs.

Each plate is developed from a vascular persistent pulp, which sends out an immense number of exceedingly long thread-like processes, which penetrate far into the hard substance of the plate. Each hair-like fibre has within its base a vascular filament or papillæ: in fact, each fibre is nothing more than an accumulation of epidermic cells, concentrically arranged around a vascular papilla, the latter being enormously elongated. The baleen plate is composed mainly of these fibres, which constitute the hairs of its frayed-out edge, but in addition to this there are layers of flat cells binding the whole together, and constituting the outer or lamellar portion. As has been pointed out by Prof. Sir Wm. Turner (Proc. Roy. Soc. Edinburgh, 1870), the whalebone matrix having been produced by the cornification of the epithelial coverings of its various groups of papillæ, is an epithelial or epiblastic structure, and morphologically corresponds not with the dentine, but with the enamel of a tooth.

The whole whalebone plate and the vascular ridges and papillæ which form it may be compared to the strong ridges upon the palates of certain Herbivora, an analogy which is strengthened by the study of the mouth of young whales prior to the cornification of the whalebone.

THE TEETH OF SIRENIA.

More nearly connected with the Ungulata than with any other order, but still rather widely removed from them, stands the limited order of Sirenia, aquatic mammals formerly termed Herbivorous Cetacea, a term rather objectionable, as they are not very nearly allied to the true Cetacea.

The order is now represented by two genera only, the Dugongs (Halicore) and the Manatees (Manatus), but a third genus (Rhytina) has only become extinct within about a century. Their teeth, and other points in their organization indicate that they are more nearly allied to the Ungulata than to any other group, though their peculiarities are such as to elevate them to the rank of a distinct order. They are of large size, and frequent shallow water, such as the mouths of great rivers, their food consisting of sea-weed and aquatic plants. Their incisors and molars when both are present are widely separated, and the former vary from being quite rudimentary to forming formidable tusks.

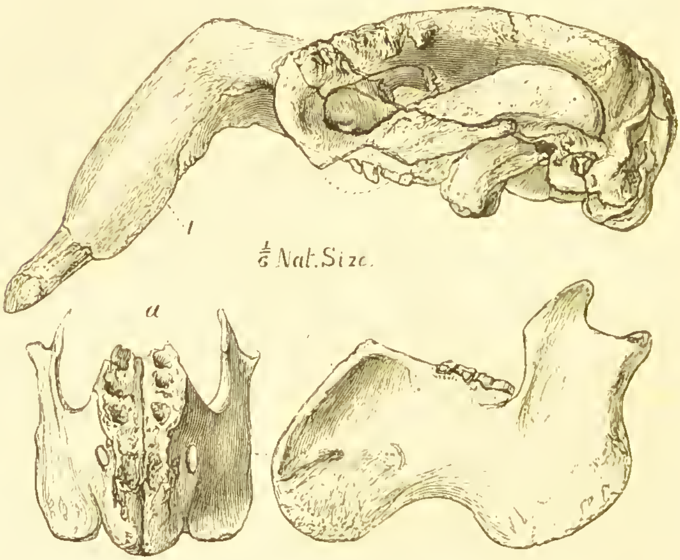
The dentition of the Dugong is in several respects a very interesting one: the front part of the upper jaw, consisting in the main of the intermaxillary bones, bends abruptly downwards, forming an angle with the rest of the jaw. This deflected end of the jaw carries two tusks, of each of which the greater part is buried within the alveolus. The tusk has an investment of enamel over its front and sides, but on the posterior surface of cementum only, so that in the disposition of the three structures it recalls the characteristics of a Rodent incisor, like which it is worn away obliquely so as to keep a constantly sharp edge, and like which it grows from a persistent pulp.

In the female, the tusks (incisors) do not project from the gum, their pulp cavities are closed, and the investment of enamel is complete over the top of the tooth.

The sloping surface of the upper jaw is opposed by the

region of the symphysis of the lower jaw, which is of unusual depth. In this deflected part of the lower jaw there are eight, or ten (four or five on each side) shallow and rather irregularly-shaped sockets, in which curved distorted

FIG. 144 (1).



teeth may be found in a fresh specimen, but it must not be from too aged an animal, as they eventually become eaten away by a process of absorption.

These abortive teeth are excellent examples of rudimentary teeth, as not only are they stunted, and even ultimately removed by absorption, but they are actually covered in by a dense horny plate which clothes this part of the jaw, and so are absolutely functionless.

(1) Side view of cranium and lower jaw of a Dugong (Halicore Indicus). From a specimen in the Museum of the Royal College of Surgeons. The surface of the deflected portion of the lower jaw, with its sockets for rudimentary teeth, shown both in front and in profile view, is indicated by the letter *a*; the corresponding surface of the upper jaw by the letter *b*.

These horny plates, in their structure analogous to whalebone, are possessed also by the Manatee and Rhytina ; on the free surface they are beset with stiff bristles, and are throughout built up of hair-like bodies welded together by epithelium.

Behind the region covered in by the horny plates, the Dugong has five molar teeth on each side, of simple form, like those of the Edentata, and consisting of dentine and cementum only.

By the time the last molar is ready to come into place, the first of the series is being removed by absorption of its root and of its socket. In aged specimens only two molars remain on each side of the jaws. Before they are worn they have tuberculated crowns and they are of semi-persistent growth.

The Dugong is also peculiar as having a single deciduous tooth : namely, a predecessor to the incisive tusks ; but it has been doubted whether it be not rather a rudimentary incisor than a milk tooth.

The molar teeth of the Manatee are much more numerous and more complex in form, and they approach to the configuration of the teeth of the Tapir very closely.

The Manatee has as many as forty-four molars, which are not, however, all in place at one time, the anterior ones being shed before the posterior are come into place ; no vertical succession is known to take place amongst them.

The Manatee has i $\frac{2}{2}$, but they are rudimentary, and are buried in the horny plates which should occupy the front of the mouth. Gervais (Hist. Nat. des Mammifères, vol. ii.) gives a larger number of rudimentary teeth, as many as twelve.

It has been mentioned that the teeth of the Manatee are tapiroid in external form ; they also possess peculiarities in minute structure, which are unusual in mammalian teeth, but which are common to them and to the Tapirs. In examining

some teeth, I found that the dentine, to all intents and purposes of the hard unvascular variety, was permeated by a system of larger, or "vascular" canals, which were arranged with much regularity, and passed out from the pulp cavity to the periphery of the dentine, where they communicated with one another. The dentinal tubes did not radiate from these vascular canals; they, so to speak, take no notice of them, so that there is an ordinary unvascular dentine with a system of capillary-conveying channels inside it. It is interesting to find that the *primâ facie* external resemblance of the teeth to those of the Tapir is fully borne out by minute histological structure, and it certainly suggests that the resemblance is not accidental, but has some deeper significance.

The enamel of the Manatee is also somewhat remarkable for the absolute straightness of its enamel prisms in many parts of the tooth.

The molar teeth of the Dugong consist of a central axis of vaso-dentine, a much larger mass of ordinary unvascular dentine, and a thick layer of cementum, but they do not share the peculiarities of the Manatee's tooth.

The Manatee has a curious manner of feeding; the halves of the upper lip, deeply cleft in the middle, are beset with short stiff bristles, and are used to tuck things into the mouth: when these fail the flappers are raised and used to assist.

The extinct Rhytina, a little more than a century ago abundant in Behring's Straits, was altogether without teeth, but was furnished with dense, strongly-ridged, horny plates. Sirenia were abundant in Miocene and Pliocene seas; the Halitherium had molars somewhat like the Manatee, but had tusk-like incisors in the upper jaw. No vertical succession is known to take place in any Sirenian, though the anterior molars of Halitherium were deciduous.

CHAPTER X.

THE TEETH OF INSECTIVORA AND CHIROPTERA.

THE Insectivora form rather a heterogeneous order of Mammals, and embrace very various forms. All of them are of rather small size, and some are very small indeed. Their diet consists for the most part of insects, and their teeth are generally adapted for this by being furnished with many points. The best known animals in the order are the Hedgehogs, the Shrews, the Moles, and the Macroscelidæ (Elephant mice) ; to these is to be added the Galeopithecus, or "Flying Lemur." Insectivora are more abundant in Africa, Asia, and South America than in Europe. The Shrews approximate in some measure towards the Rodents, and the Tupaia is very lemurine in its characters.

They all have small brains, and long faces. The Insectivora are ancient and in some respects rather generalised mammals, so that they may be supposed not to have diverged far from the parent forms of other mammalia. Prof. Cope has described a good many genera which have been found in American Eocene Strata, and some of these, *e.g.*, Mesonyx, had teeth differentiated into incisors, large canines, premolars and molars, but these last two were of simple form, being in the lower jaw cones, with slight anterior and posterior cusps added by elevations of the cingulum.

The upper molars had crowns which were rendered triangular upon the grinding surface by the development of an internal cusp.

Its dental formula was

$$i\,\frac{3}{2}\,c\,\frac{1}{1}\,pm\,\frac{4}{4}\,m\,\frac{3}{3}.$$

Of the teeth of Insectivora generally it may be said that it would not be difficult to imagine how the teeth of all other Diphyodont Mammals might be evolved from them, whilst Prof. Cope (Proc. Acad. Nat. Sc. Philadelphia, 1883, and passim; see also D. Wortman, Americ. System Dental Surgery, Teeth of Vertebrata) gives an admirable series of extinct genera in which the molar patterns become more complex, and approximate on the one hand to the sectorial teeth of Carnivora, and on the other to the bristling cusps of modern Insectivora.

Galeopithecus stands alone: it was formerly, and is indeed sometimes even now, placed with the Lemurs; but it has much more in common with Insectivora. The teeth are somewhat anomalous, the lower incisors being divided by a number of vertical divisions running down through a great part of the length of the crowns, so that they can be compared to combs, or to hands with the fingers slightly separated. What the purpose served by these comb-like teeth may be remains uncertain: no other animal has similar teeth. Galeopithecus has a well developed milk dentition, the milk teeth being very similar to their successors.

The dental formula is

$$i\,\frac{2}{3}\,c\,\frac{1}{1}\,pm\,\frac{2}{2}\,m\,\frac{3}{3},$$

and the second upper incisor and the canine are two-rooted.

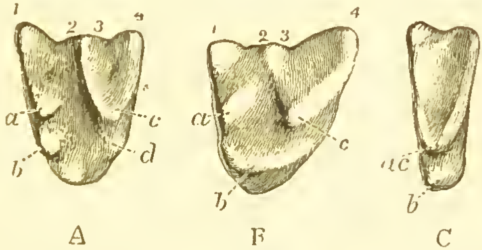
Excluding Galeopithecus, the others are divided into two groups by the patterns of the molars; the majority present a **W**-pattern (Tupaia, Macroscelis, Erinaceus, Sorex, Talpa), whilst the other group have narrower molars with a **V**-pattern (Potaomgale, Centetes, Chrysochloris).

The **W**-pattern characterising the molars of Insectivora is well exemplified in the molar of Urotrichus.

In this tooth, as has been clearly shown by Prof. Mivart (Osteology of Insectivora, Journ. of Anat., 1868), the four cusps of the typical teeth (*a*, *b*, *c*, *d*) have been added to by the elevation of the cingulum into three or four external, and one internal cusp, making up the total number to nine. Thus it is that the molars of this order often fairly bristle with cusps.

In the Mole the number of cusps is diminished by the coalescence of *b* and *d* into a ridge, and the disappearance of

Fig. 145 ([1]).



the inner cusp of the cingulum, while the simplification is carried yet further in the Cape Mole (*c* in Fig. 145).

The common English Hedgehog (Erinaceus) has the dental formula

$$i\,\frac{3}{2}\;c\,\frac{0}{0}\;pm\,\frac{4}{3}\;m\,\frac{3}{3}.$$

In the upper jaw there is a wide interval between the first pair of incisors, which are much the largest, and are caniniform in shape. The next two teeth (incisors) are quite small, and resemble premolars in their form. The next tooth has two roots, and a crown with one cusp, and is

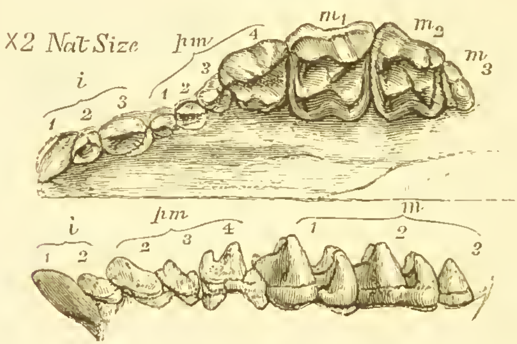
([1]) Upper molar teeth of (A) Urotrichus ; (B) Mole ; and (C) Chrysochloris. The four principal cusps are lettered *a*, *b*, *c*, *d*, in each of the figures. In A the cingulum has been elevated so as to form four additional cusps on the exterior of the tooth, and one additional cusp on the interior. B and C show the fusion of certain of these cusps, and the consequent diminution in their number. (From Mivart.)

also like the premolars behind it. This tooth, the root of which shows indications of division, is sometimes called a canine, because it comes next behind the intermaxillary suture; behind this come two small premolars.

The fourth upper premolar is totally different in size and form from the third: its crown is large, squarish, and furnished with four cusps, of which the antero-external one is far the longest and sharpest.

The first upper true molar has a square crown, upon which are four sharp cusps: it is implanted by four roots.

Fig. 146 (1).



The second true molar is also square, quadricuspid, and has four roots; but it is much smaller than the first, while the third upper true molar is quite a small, compressed, double-rooted tooth, with a thin-edged crown.

In the lower jaw the first incisors, less widely separated than the upper, are also the largest; then follows another tooth termed incisor, on account of its relation to the upper incisors when the mouth is closed. The third tooth is much larger, and of peculiar form. The fourth tooth from the front is a small single tooth, like the third, but upon a smaller scale. Next behind it, comes a tooth which is very

(1) Upper and lower teeth of the Hedgehog.

much larger, and its crown carries two principal cusps with a small subsidiary cusp. The next tooth (first true molar) has an oblong crown beset with five sharp cusps, of which four are arranged at the corners of a square, while the fifth, obviously an elevation of the cingulum, lies a little in front and towards the inside of the tooth. In the second true molar the fifth cusp is but little indicated, while the last true molar is a dwarfed tooth with but one cusp. Several dental formulæ have been assigned to the Hedgehog: there is little room for difference of opinion as to the nomenclature of its upper teeth: though some authors (*e.g.*, Professor Mivart) prefer to call the first premolar a canine. But in the lower jaw some authors give i $\frac{-}{2}$ c $\frac{-}{1}$ pm $\frac{-}{2}$, others i $\frac{-}{3}$ c $\frac{-}{0}$ pm $\frac{-}{2}$, and others again, i $\frac{-}{2}$ pm $\frac{-}{3}$. The last given seems the least artificial, and corresponds best with the relations between the upper and lower teeth when the mouth is closed.

Rousseau describes the existence of twenty-four milk teeth, which he classifies thus: (i $\frac{3}{4}$ dm $\frac{4}{1}$); that is to say, all the teeth in front of the true molars had deciduous predecessors, but his grouping of them into incisors and molars is quite arbitrary.

The milk teeth are not shed and replaced until the animal has attained to almost its full dimensions, and all three true molars are in place.

The teeth of the Hedgehog fairly represent some of the features of Insectivorous dentitions, for the forcep-like incisors, the stunted or non-developed canines, and the molars bristling with pointed cusps, are common to very many of the order.

The Shrews have numerous sharply-pointed teeth, the points interdigitating and fitting very closely together

when the mouth is shut. There is no tooth either in the upper or lower jaw which is so elongated as to deserve the name of canine; but between the incisors and the true molars are several small teeth which, by analogy, are called premolars. The true molars are not very different in pattern from those of the mole (B in Fig. 130), and present the **W**-contour so common in the molars of Insectivora.

The most marked peculiarity in the dentition of the Shrews lies in the form of their incisors. The first upper incisor is always very large indeed: it looks vertically downwards, is a little hooked, and has a notch, and a second low cusp behind the principal long pointed cusp. The tip of the lower incisor fits into this notch. The lower incisor is also very large; it lies nearly horizontally, though the point is bent a little upwards. Along its upper edge there are, in most species, three or four small cusps, while its lower border is curiously prolonged outside the bone of the jaw, so as to in some measure encase this latter. The lower incisor is at least one-third as long as the whole alveolar border. The incisor teeth of the Shrew would appear to form a very efficient pair of pincers, with which to pick up the minute creatures on which it feeds. Of the milk teeth of Shrews little is known: they are said to be absorbed before birth, but accurate observations upon them are much needed, their very existence being doubtful.

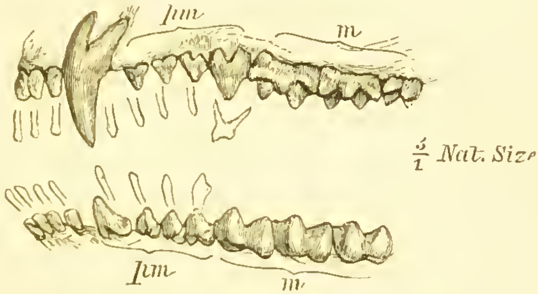
The dentition of the Mole (Talpa) has been the subject of much controversy, the determination of its canines, &c., presenting such difficulty that no less than five different dental formulæ have been assigned to it.

In the front of the upper jaw come three small teeth, the first being somewhat the largest, which are well within the limits of the intermaxillary bone, and are doubtless incisors. But the next tooth, which is very big, also appears to be implanted in the intermaxillary bone, the suture passing across its socket close to the back of its posterior root.

According to its implantation it therefore would be an incisor (1) but it is very unlike an incisor; and it is two-rooted, a thing anomalous either in an incisor or a canine, though found in the canine of Gymnura, which is beyond question in the maxillary bone.

Next come three minute premolars, and a fourth, which is much larger than the others: these all have simple

Fig. 147 (2).



crowns, consisting of little more than a single sharply-pointed cusp.

The first two upper molars are large teeth bristling with cusps: the third is much reduced in size and simplified in pattern. In the lower jaw the *four* front teeth are all small, but the fourth or outermost of these incisors is called by some writers the lower canine, because, when the teeth are closed, it passes in front of the upper caniniform tooth.

(1) The late Mr. Spence Bate, in his valuable paper on the milk teeth of the mole, says, "This tooth is implanted within the limits of the pre-maxillary bones, the suture separating them from the maxillary, passing through the posterior portion of its alveolus: *thus demonstrating that this deciduous tooth is the true homologue of that of the canine in the mammalian type.*" Surely it would go to prove the contrary, if accepted as evidence at all upon this point.

(2) Upper and lower teeth of the common Mole. The functionless milk teeth (after Spence Bate) are placed above the permanent teeth which displace them.

Nevertheless the tooth which does the work of a canine in the lower jaw is the fifth counting from the front : this is a two-rooted tooth, and conforms so closely with the three teeth behind it in configuration, that it is obviously only one of these premolars developed to a greater length than the others. It closes *behind* the caniniform upper tooth, so cannot on this ground be called a canine by those who attach importance to the term.

The remaining three premolars are rather small and single; the true molars are of considerable size, and their points are very long and sharp.

I have purposely avoided giving any dental formula for the Mole : everything turns upon the value which we attach to the term canine; and I have already given reasons for attaching but little homological importance to its determination.

The late Mr. Spence Bate's paper (Trans. Odontol. Society, 1867), valuable as it is in contributing to our whole knowledge of the milk dentition of the creature does not finally determine the homologies of the canine.

In a Mole $3\frac{3}{4}$ inches long he found eight milk teeth on each side of both upper and lower jaws, as is indicated in Fig. 147. The milk incisors were about one-twentieth of an inch in length, and one two-hundredth in diameter, and were rudimentary in form, consisting of long thin cylindrical tubes surmounted by slightly expanded crowns. All the milk teeth were of this simple form, save only the last in each jaw, which presented crowns with two cusps, and had their roots to some little extent divided into two.

At the time when these teeth are present the intermaxillary suture is very distinct, and there is no doubt that the fourth upper milk tooth, the predecessor of the caniniform tooth, is in the intermaxillary bone.

The teeth had not fairly cut the gum, and the advanced state of the permanent teeth beneath them make it doubtful

whether they ever do become erupted. At all events, they can be of no use.

In many of the order Insectivora the milk dentition is unknown, but we have exemplified amongst them every grade of completeness in its development. Thus in the Hedgehog and Centetes (an allied animal from Madagascar) the milk dentition is tolerably complete, while in the Shrews it has all but, or quite, disappeared.

The teeth of Insectivora are remarkable for the thickness of their enamel, which in the Shrews is to some extent penetrated by the dentinal tubes. The enamel is deeply coloured in some Shrews, the pigment being actually in the substance of the enamel, and not in any distinct layer.

THE TEETH OF CHIROPTERA.

The Bats, sharply distinguished from all other mammals by the possession of wings, are divided into two groups, respectively insectivorous and frugivorous.

The insectivorous Bats, by far the most numerous section, are for the most part possessed of small incisors, rather large canines, and premolar and molar teeth which bristle with sharp cusps, and generally present the W-pattern. In fact, in general character, their teeth resemble those of the Insectivora, but the dental formula never exceeds—

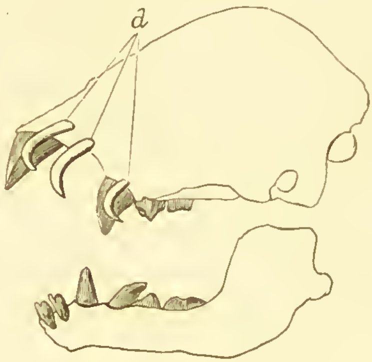
$$i\,\frac{2}{3}\;c\,\frac{1}{1}\;pm\,\frac{3}{3}\;m\,\frac{3}{3}.$$

The incisors are sometimes reduced in number, and spaces left between them; and some, as for example, the Vampire (Desmodus) have teeth specially modified to accord with their blood-sucking habits.

This Bat has only one permanent incisor on each side, and this is a large but thin and sharp-edged tooth, with which

the wound is made; the lower incisors are small teeth with feebly notched edges. The canines are large, and the molar

FIG 148 (1)



series, which is not required in an animal existing upon blood, is stunted. The molar teeth are, however, sharp, though small, and there is no marked distinction into molars and premolars: the dental formula is—

$$i\,\frac{1}{2}\;\;c\,\frac{0}{0}\;\;pm\,\frac{2}{3}\;m\,\frac{0}{0}\text{ or }\frac{1}{1}.$$

The frugivorous bats (of which the Pteropus, or flying fox, is an example) have much larger muzzles, and the molar teeth are set with intervals between them.

The dental formula is $i\,\frac{2}{2}\;c\,\frac{1}{1}\;pm\,\frac{2}{3}\;m\,\frac{3}{3}$, but in some the molar series is reduced below this number.

The incisors are small, and the canines rather large.

Both molars and premolars are of somewhat simple form, being long, and compressed from side to side. The outer borders of the crown of the molars are elevated into distinct but not exceedingly sharp cusps, which become worn down by use.

(1) Skull of Desmodus, showing milk teeth.

The insectivorous character of the presence of many sharp cusps upon the teeth is not to be found in any of the frugivorous bats. All the Pteropi have deciduous canines, and four deciduous molars, of simple pointed form, but the number of deciduous incisors is very variable.

The milk dentition of bats has been very carefully and thoroughly investigated by Leche (Lund's Universit. Ars-skrift, Tom. XII. and XIV., 1878), and at the present the Megadermata are the only family in which the milk teeth are unknown. The milk teeth are not of much functional importance, as they are shed soon after, if not absorbed before, birth, and they are not therefore implanted in very definite sockets.

In their slight cylindrical elongated roots, surmounted by expanded crowns, these milk teeth often recall those of the Mole.

Sometimes the milk teeth are to be found even after the permanent teeth are *in situ;* in other instances, as for example the deciduous molars of Molossus, they never cut the gum. The milk dentition of the Vampire (Desmodus) (1) appears to consist of incisors only, or of incisors and canines; though the absence of observed molars may be due to the fact that they are, as in Molossus, shed very early.

It has, near to the front of the upper jaw, six teeth, each of which is very long and slender, and has a strongly hooked point: it has been suggested that these feeble hooked teeth may assist it in holding on to the mother.

In general terms it may be said that the milk teeth of the majority of Chiroptera do not at all resemble their permanent successors.

(1) In a skull of Desmodus, in the possession of Mr. R. F. Tomes, the third milk tooth appears to correspond in position to the permanent canine; the same is the case in the specimen figured by Messrs. Gervais and Castelmain (Exped. dans les part. cent. d'Amérique du Sud).

An anomalous dentition has been found in a New Guinea Bat, in which the canines, whilst having a long principal cusp, are rendered multi-tuberculate by other cusps at their base, this pattern being more or less repeated in the other teeth. (Oldfield Thomas, Proc. Zool. Society, 1889.)

THE TEETH OF RODENTIA.

The animals belonging to this order, which is sharply defined, are scattered almost all over the world ; the island of Madagascar is, however, remarkable for being almost without indigenous Rodents, as is the case also with Australia, two facts which are of no small interest to the student of odontology.

For in each of these areas, out of the creatures which are there (in the one Lemurs, in the other Marsupials), there has arisen a form so modified as to mimic and take the place of the true Rodents, viz., the Cheiromys in Madagascar, and the Wombat in Australia.

The species of Rodents are exceedingly numerous, and the great majority of them are of small size ; the aquatic Capybara is far the largest of recent Rodents.

An average Rodent dentition would be

$$i\,\frac{1}{1}\;c\,\frac{0}{0}\;pm\,\frac{1}{1}\text{ or }\frac{0}{0}\;m\,\frac{3}{3};$$

as extremes the Hare has

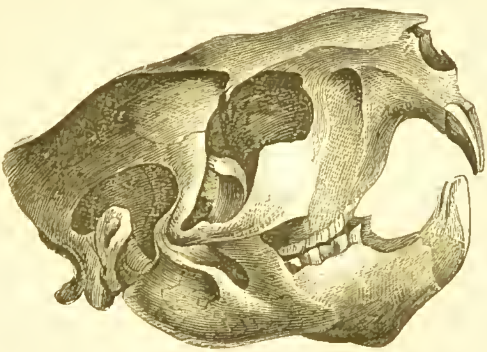
$$i\,\frac{2}{1}\;c\,\frac{0}{0}\;pm\,\frac{3}{2}\;m\,\frac{3}{3},$$

and Hydromys

$$i\,\frac{1}{1}\;c\,\frac{0}{0}\;pm\,\frac{0}{0}\;m\,\frac{2}{2}.$$

In general features the dentitions of the numerous speeies eomprising this order are very uniform ; the ineisors, (save in the hares and rabbits, in whieh there is an aeeessory small pair immediately behind the large ones) are redueed to four in number, are of very large size, and grow from persistent pulps. The jaws for some little distanee behind the ineisors are devoid of teeth, while beyond the interval the baek teeth, generally not more than four in number, are arranged in lines whieh diverge slightly as they pass baekward. The large sealpriform, or ehisel-like ineisors, extend far baek into the jaws, and are mueh eurved, the

Fig. 149 ([1]).



upper ineisors, in the words of Professor Owen, forming a larger segment of a smaller eirele than the lower, which are less eurved. The length and eurvature of these ineisors relieve from direet pressure their growing pulps, whieh eome to be situated far back in the jaw, the open end of the lower incisor, for example, being in many species aetually behind the last of the molar teeth. The nerve going to supply the persistent pulps is of very large size, and, owing to the open end of the tooth having formerly oeeupied a

([1]) Side view of skull of a Rodent, giving a general idea of the dentition of the order.

more anterior position in the jaw, runs forward beneath the tooth, and then bends abruptly backwards to reach the tooth-pulp. In many Rodents the enamel of the front of the large incisors is stained of a deep orange colour; this colour is situated in the substance of the enamel itself.

The scalpriform incisors terminate by cutting edges, the sharpness of which is constantly maintained by the peculiar disposition of the tissues of the tooth.

The investment of enamel, instead of being continued round the whole circumference of the tooth, is confined to its anterior and lateral surfaces, on the former of which it is thickest.

It is, however, stated that the enamel organ is continued round the roots, so that the connective tissue bundles by which attachment to the cementum is made, have to grow through it to take their hold. (v. Brunn.)

It is said by Hilgendorff (Berlin Akad. d. Wiss. Monatsbericht, 1865), that the incisors of hares differ from those of all other Rodents in having enamel all round them, although it is very thin at the back. I have not been able to satisfy myself that the thin clear layer at the back of the tooth is enamel, and am disposed to regard it as cementum, the more so as it seems to be continued a little way upon the enamel, and in very young teeth the large cells of the enamel organ are confined to the anterior surface. (1)

When a Rodent incisor has been exposed to wear, the anterior layer of enamel is left projecting beyond the level of the dentine, and this arrangement results in a very sharp edge being constantly maintained. The dentine also is harder near to the front of the tooth than towards the back of the tooth.

A thin external coat of cement is found upon the back of the tooth, but is not continued far over the face of the enamel. In the marsupial wombat this layer of cement is

(1) Cf. E. G. Betts, Trans. Odontological Society, May, 1884.

continued over the whole anterior surface of the scalpriform incisors.

The molar teeth are not very numerous; the mouse family have usually $\frac{3}{3}$; the porcupines have constantly $\frac{4}{4}$, and the hares $\frac{6}{5}$; the Australian water-rat (Hydromys) is altogether exceptional in having so few as $\frac{2}{2}$. Observation has established that the last three of these teeth are always true molars, and that when there are more than three, the rest are premolars, and have had deciduous predecessors.

But the extent to which the milk teeth are developed varies much. Mr. Waterhouse (Nat. Hist. of Mammalia—Rodents, p. 4), has found the milk molar still in place in the skull of a half-grown beaver, while in the hares they are shed about the eighteenth day after birth, and in the guinea-pig disappear before birth. Deciduous incisors have not been found in any of the group, save in the hares and rabbits.

In the hares and rabbits there are four incisors in the upper jaw, a small and apparently functionless pair being placed close behind the large rodent incisors; but in very young specimens there are six incisors, of which the one pair are soon lost.

Prof. Huxley (Nature, vol. 23, p. 228) has recently written that "the deciduous molars and the posterior deciduous upper incisors of the rabbit have been long known. But I have recently found that unborn rabbits possess, in addition, two anterior upper and two lower deciduous incisors. Both are simple conical teeth, the sacs of which are merely embedded in the gum. The upper is not more than one-hundredth of an inch long, the lower rather larger. It would be interesting to examine fœtal guinea-pigs in relation to this point; at present they are known to possess

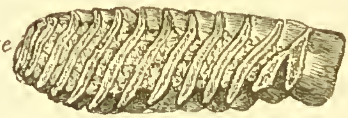
only the hindmost deciduous molars, so far agreeing with the Marsupials."

Hares and rabbits have six milk molars in the upper and four in the lower jaw, which come into use, but differ from their successors in forming definite roots and not growing from persistent pulps.

Other Rodents, such as the rat, which has only three teeth of the molar series on each side, and the Australian

Fig. 150 (1).

Nat. Size



water-rat (Hydromys) have no known milk teeth, and are hence perhaps truly Monophyodont.

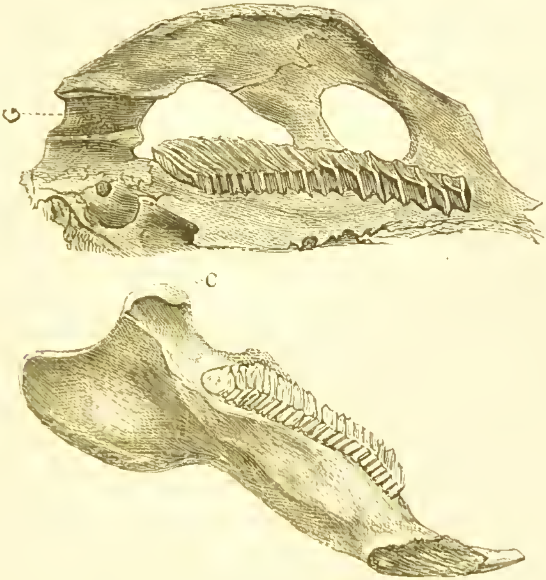
More diversity exists in the premolar and molar teeth; in Rodents of mixed diet, such as the common rat, the back teeth are coated over the crown with enamel, which nowhere forms deep folds, and have distinct roots, *i.e.*, are not of persistent growth; the molars of the rat have some sort of resemblance to minute human molars. In aged specimens the enamel is consequently worn off the grinding surface of the crown, which comes to be an area of dentine, surrounded by a ring of enamel.

But in those whose food is of a more refractory nature, the molars, like the incisors, grow from persistent pulps (as is exemplified in the Capybara here figured), and their working surfaces are kept constantly rough by the enamel dipping in deeply from the side of the tooth, as may also be seen in the common water-rat. The inflection of enamel

(1) Molar of Capybara, showing the transverse plates of dentine and enamel united to one another by cementum.

may be so deep as to divide the areas of dentine completely up, the result being a tooth like that of the Capybara, which is composed of a series of plates of dentine, or 'denticles,' surrounded by layers of enamel, and all fused together by the cementum. The result of this disposition of the struc-

Fig. 151 (1).



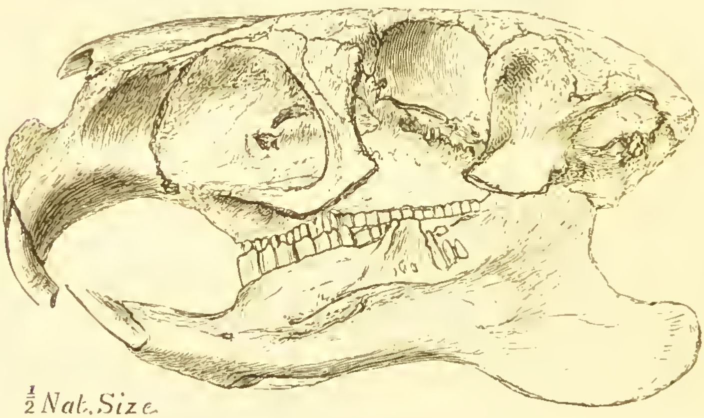
tures is that the working surface is made up of enamel, dentine, and cementum, three tissues of different hardness, which will consequently wear down at different rates, and so maintain its roughness. Various intermediate forms of the molar teeth are met with; thus there are some in which complexity of the surface is maintained by folds of enamel dipping in for a little distance, but which nevertheless after a time form roots and cease to grow. When the molar teeth grow from persistent pulps, they are always curved, like the incisors, with the effect of relieving the

(1) Condyle and glenoid cavity of the Capybara, showing their longitudinal direction.

pulps from direct pressure during mastication; and the last remains of the pulps are converted into secondary or osteo-dentine, which thus forms the central axis of the incisors, or molars, as the case may be. In this tissue vascular tracts sometimes exist, but it is altogether small in amount, the formation of true dentine going on till the pulp at that particular point is almost obliterated.

As has already been mentioned, when the molar series

Fig. 152 (1).



½ Nat. Size.

consists of more than three teeth, those anterior to the three true molars are premolars, which have displaced milk teeth; but they do not differ materially in size or form from the true molars.

The form of the condyle and of the glenoid cavity in Rodents are characteristic; they are much elongated in an antero-posterior direction, so that the range of backward and forward motion, made use of in gnawing, is very considerable. The Leporidæ are exceptional in having more lateral play than most Rodents. And the power of the teeth is marvellous; rats will sometimes gnaw holes in

(1) Cranium of Capybara.

water-pipes, or in gas-pipes, in which they have heard water bubbling.

The general character of a Rodent's dentition may be illustrated by a description of that of the Capybara.

The incisor teeth are squarish. They are wider than they are deep, and are slightly grooved on their anterior surface.

There are four grinding teeth on each side, of which the first three are small, and with few cross plates of dentine and enamel, but the fourth is a very complex tooth, with twelve or more such plates, which are fused into a solid mass by cementum.

This tooth being one of persistent growth, there is no common pulp cavity, but each plate has its own.

It has already been mentioned (page 170) that the dentinal tubes at that part of the Rodent's incisor which has come into use are much smaller than those near to its growing base, thereby proving that they have undergone a diminution in calibre at a time subsequent to their original formation. Near to the surface actually in wear they become cut off from the pulp cavity by the conversion of what remains of the pulp into a laminated granular mass, so that the dentine exposed on the surface of a Rodent's tooth must be devoid of sensitiveness, and the contents of the dentinal tubes must have presumably undergone some change. But what the nature of the change in the contents of dentinal tubes which have ceased to be in continuity with a vascular living pulp may be, there are, so far as I know, no observations to indicate.

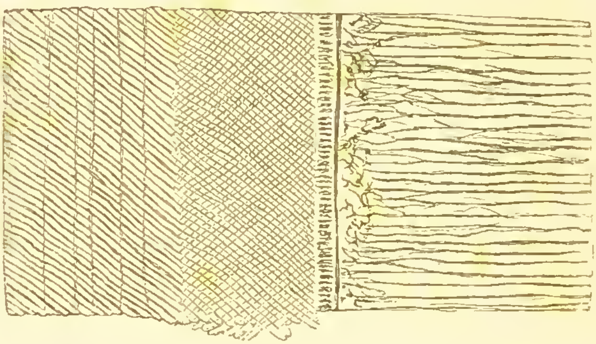
As was shown by my father (Phil. Trans. 1850), the enamel of Rodents is peculiar, and some little diversity in the arrangement of the prisms exists in different families of the order, their character being in many cases so marked, that it is often possible to correctly refer a tooth to a particular family of Rodents after simple inspection of its enamel.

In general terms it may be said that the enamel is divided into two portions, an outer and an inner portion (this is true of all save the hares and rabbits), and that the enamel prisms pursue different courses in these two portions.

Thus in the enamel of the beaver, in the inner half, nearest to the dentine, the prisms of contiguous layers cross each other at right angles, whereas in the outer portion they are all parallel with one another.

In the genera Sciurus, Pteromys, Tamias, and Spermophilus the enamel fibres, as seen in longitudinal section,

FIG. 153 (1).



start from the dentine at right angles to its surface; in Castor they incline upwards at an angle of 60°, but preserve the distinction between the outer and inner layers very distinctly.

In the Muridæ the decussation of the layers in the inner part, and their parallelism in the outer part of the enamel are also found, but in addition to this the borders of the individual prisms are slightly serrated, the serrations of contiguous fibres interlocking.

In the porcupine sub-order the fibres of the inner portion

(1) Transverse section of an incisor of a Beaver (Castor fiber). The enamel prisms of superimposed layers cross each other at right angles in the inner portion of the enamel, but all become parallel in the outer.

of the enamel pursue a serpentine course, nevertheless showing indications of a division into layers; they become parallel in the outer portions as in other Rodents. Small insterspaces are found amongst the enamel fibres of the porcupines.

In the hares (Leporidæ) the lamelliform arrangement, and the division into outer and inner layers, alike disappear.

The peculiarities in the disposition of the enamel fibres, which are so marked in the incisors, do not generally exist in the molars of the same species.

Many minor differences in the arrangement of the enamel prisms exist, for a description of which I must refer the reader to the original paper, but in general terms it may be said that the "enamel lamellæ have a different and distinctive character in each of the larger groups, and that the variety of structure is constant throughout the members of the same group; we may take, for example, the Sciuridæ, the Muridæ, and the Hystricidæ, in each of which the structure of the enamel is different; and in each is highly distinctive." And further, that the varieties in the structure of the dental tissue, so far as they are known, with a few isolated exceptions, justify and accord with the classification of the members of the order usually given.

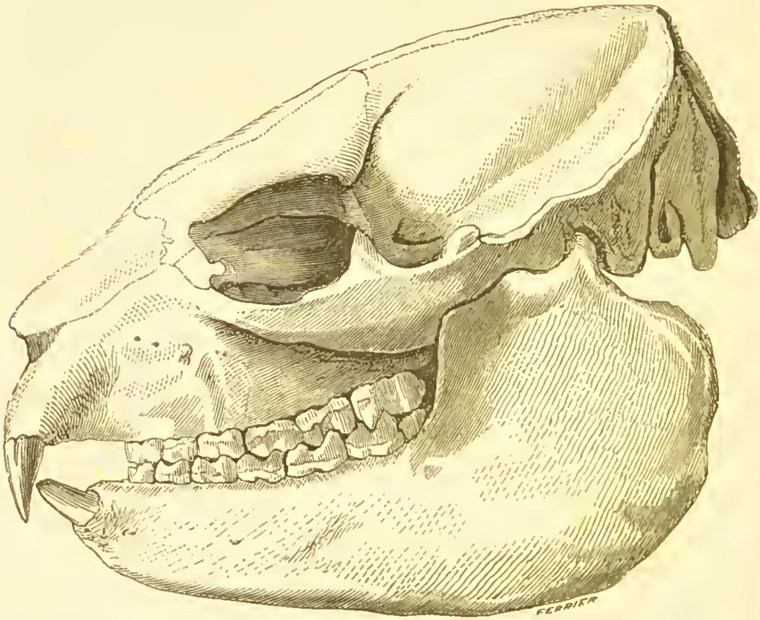
THE TEETH OF HYRACOIDEA.

The Biblical coney (Hyrax), an animal as large as a rabbit, must not be passed over without mention, as its dentition has been indirectly the source of much controversy. So far as the pattern of its molar teeth goes, it corresponds closely with Rhinoceros, and was hence classed in close proximity to that genus by Cuvier. But a more extended survey of its characters has led to its being placed

in a separate sub-order ; it is a good example of the danger which attends relying upon any single character, such as the pattern of the teeth, as being alone a sufficient basis for classification.

All observers, however, are not agreed as to its position

FIG. 154 (1).



it certainly presents affinities with Perissodactyla, but most modern zoologists are pretty well agreed in placing it in a sub-order by itself. Prof. Cope, however, regards it as closely akin to some early highly generalised Ungulates, which he groups together by the name of Taxeopoda; they all possessed five toes on each foot, and many of the characters of their teeth bring them within measurable distance of ancient Insectivora.

(1) Skull of the Hyrax.

The dental formula is $i\,\frac{2}{2}\; c\,\frac{0}{0}\; pm\,\frac{4}{4}\; m\,\frac{3}{3}$.

Seen from the side, the dentition bears some resemblance to that of a Rodent, because of the large size of its central incisors, which grow from persistent pulps, are chisel-edged, prismatic in section, and are furnished with a very thick coat of enamel on their antero-external and antero-internal faces: the second pair of incisors, which are small, are soon lost. But Hyrax has the full typical number of premolars and molars, and the patterns of these teeth are closely similar to those of the Rhinoceros.

In the lower jaw the middle incisors are small, and the outer ones largely developed, and all persist: their crowns are in a manner trilobed, and they pass in ordinary closure of the mouth behind the upper incisors, where they are met by a dense pad of gum, but they are not of persistent growth.

THE TEETH OF PROBOSCIDEA.

At the present day the Elephant stands alone, removed by many striking peculiarities from the Ungulata, to which it is more nearly allied than to other orders; but in former days the order Proboscidea was represented by a good many genera, was widely distributed over the globe, and transitional forms linking the elephant with somewhat less aberrant mammalia were not wanting. In this group the incisors grow from persistent pulps, and form conspicuous tusks; the elephant has $i\,\frac{1}{0}$, the Mastodon has $i\,\frac{1}{1}$, the Dinotherium $i\,\frac{0}{1}$.

Two striking features characterise the dentition of the elephant; the enormous length of the incisor tusks, and

the peculiar displacement from behind forwards of the molar teeth, by which it results that not more than one whole molar, or portions of two, are in place at any one time.

The upper tusks are preceded by small deciduous teeth; this is well established, though it has been recently denied by Sanderson (Wild Beasts of India). When first cut they are tipped with enamel, but the enamel cap is soon worn off, and the remainder of the tusk consists of that modification of dentine known as "ivory," and of a thin external layer of cement. In some extinct species the enamel formed longitudinal bands upon the tusks.

In the Indian elephant the tusks are not so large as in the African species: and the tusks of the female are very much shorter than those of the male. In the African elephant, no such difference in size has been established; and amongst Indian elephants males are sometimes met with which have tusks no larger than the females of corresponding size; they go by the name of "Mucknas." This peculiarity is not always transmitted, and it is known that in Ceylon tuskless sires sometimes beget "tuskers." Amongst the Ceylon elephants the possession of large tusks by the male is an exceptional thing, Sanderson stating that only one in three hundred has them, while amongst 51 Indian elephants only five were tuskless. The tusks are formidable weapons, and great dread of a "tusker," is shown by elephants less well armed.

A male makes use of his tusks for all sorts of purposes; thus when a tamed one is given a rope to pull, he will, by way of getting a good purchase upon it, pass it over one tusk and grasp it between his molar teeth.

A pair of African tusks exhibited at the Great Exhibition of 1851 weighed 325 lbs., and measured 8 feet six inches in length, and 22 inches in circumference, but the average tusks imported from Africa do not exceed from 20 lbs. to 50 lbs. weight. Indian elephants seldom have tusks attain-

ing very large dimensions; one was, however, shot by Sir Victor Brooke with a tusk 8 feet long, weighing 90 lbs.

The largest tusks were possessed by the Mammoth, the remains of which are so abundant in Siberia; these, which are strongly curved, and formed a considerable segment of a circle with an outward inclination, so as to well clear the sides of the head, attained the length of 13 feet, and a weight of 200 lbs. each.

Ivory is one of the most perfectly elastic substances known, and it is on this account that it is used for billiard balls; it owes its elasticity to the very small size of the dentinal tubes and the frequent bends (secondary curvatures) which they make; to the arrangement of the tubes the peculiar engine-turning pattern of ivory is due. It differs from other dentine in its containing from 40 to 43 per cent. of organic matter (human dentine contains only about 25), and in the abundant concentric rows of interglobular spaces. Along these ivory when it decomposes breaks up, so that a disintegrated segment of a tusk consists of detached concentric rings; in this condition many mammoth teeth are found, although sometimes where they have remained frozen and protected from the air until the time of their discovery they are hardly affected by the lapse of the thousands of years which have gone by since their possessors perished.

The best ivory is that which comes from equatorial Africa; Indian ivory is not so highly esteemed, and mammoth ivory is so uncertain in its degree of preservation that it does not find a ready sale, even though some samples almost attain the quality of recent ivory.

The last remains of the pulp are converted into dentine in which a few vascular canals persist; this of course occupies the centre of the tusk, and is small in amount.

The trade in ivory is quite an important one, the Board of Trade returns for 1879, giving 9414 cwts., of

the value of £406,927, as the quantity brought to this country.

But the best of mammoth ivory, which has been preserved by the low temperature from any change, so that it is hardly distinguishable from recent ivory, has long been an article of commerce, perhaps even from the time of Pliny.

Nordenskiöld (Voyage of the Vega) mentions that the dredge often brought up portions of tusks, and the natives offered at times very fine tusks for sale.

It is estimated that 100 pairs annually come thus into the market, and this is probably less than the real number. He travelled up the Yenisei in 1875 on board a steamer which carried over 100 tusks, of which, however, a large number were so blackened and damaged, that it was difficult to suppose them marketable.

The nearer you get to the Polar coasts the more abundant are the mammoth remains, especially where there have been great landslips, though the tusks found at the lowest latitudes are said to be smaller.

In the new Siberian Islands, in the space of a verst, he saw ten tusks sticking out of the ground, and from a single sand-bank ivory collectors have for eighty years reaped a harvest.

In England dealers in ivory seem all to deny ever using mammoth ivory, though the finest specimens require the eye of an expert to distinguish them from recent ivory when cut up, and the denial must be taken *cum grano.*

The surfaces of the tusks of the female are often deeply excavated about the level of the edge of the gum, and are sometimes so weakened from this cause that they break off. My friend Prof. Moseley tells me that he was informed by the late Major Rossall, who as a sportsman had great knowledge of Indian elephants, that the tusks of all the females he has ever seen are so affected, and that the larvæ or pupæ of a dipterous insect are often found bedded in the gum, and

attached to the surface of the tusk. There is a specimen of a female elephant's tusk with the pupæ attached in the Museum of the Royal College of Surgeons. It would be a matter of interest to ascertain whether the larva really eats away the tusk, or whether the wasting of the tusk be due to absorption set up by the irritated gum.

The tusks of an elephant are implanted in long and stout sockets, and grow from persistent pulps throughout the lifetime of the animal.

In the Indian elephant about one half of the length of the tusk is implanted, and in young animals the pulp cavity extends beyond the implanted portion, but in older animals it does not extend nearly so far. A knowledge of its extent is necessary, seeing that the tusks of captive elephants have to be shortened from time to time; this operation is by some done frequently, by others only at long intervals, such as ten years, in which case a large and valuable segment of ivory is cut off, and the end of the tusk bound with metal to prevent it from splitting.

Tusks sometimes exemplify on a large scale the results of injury to the growing pulp, as it is of no unfrequent occurrence that elephants which have been shot at and wounded escape.

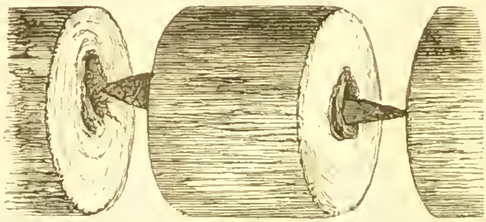
The thin walls of the tusk near to its open end do not offer very much resistance to the entrance of a bullet; the result of such an injury is not, as might have been expected, the death of the pulp, but in some cases abscess cavities become formed in the neighbourhood of the injury, while in others less disturbance is set up, the bullet becomes enclosed in a thin shell of secondary dentine, or sometimes lies loose in an irregular cavity, and round this the normal "ivory" is deposited; upon the outside of the tusk no indication of anything unusual is to be seen, so that the bullets thus enclosed are found by ivory turners only when sawing up the tusk for use.

As the tusk grows, that which was once in the pulp cavity, and within the alveolus, comes to be at a distance from the head, and in the midst of solid ivory.

As an example of the extent of injury from which a tooth pulp is capable of recovery, may be cited a specimen now deposited in the Museum of the Odontological Society, by Mr. Bennett, to whom I am indebted for permission to figure it.

It is to be presumed that a trap was set with a heavily loaded spear, or that it was dropped by a native from a tree, with the intention of its entering the brain of the

Fig. 155 [1].



elephant as it was going to water, both of these methods of killing elephants being practised in Africa. But in this case the spear penetrated the open base of the growing tusk, which looks almost vertically upwards (see fig. 155), and then the iron point appears to have broken off. This did not destroy the pulp, but the tooth continued to grow, and the iron point, measuring no less than $7\frac{1}{2}$ by $1\frac{1}{2}$ inches, became so completely enclosed that there was nothing upon the exterior of the tusk to indicate its presence.

I am told by Mr. Erxleben that he is acquainted with another instance in which a spear head has become completely enveloped in ivory.

[1] Iron spear-head, irremovably fixed in the interior of a tusk, believed to be from an African Elephant. From a specimen in the possession of Mr. Bennett.

There are also other specimens extant, of which an excellent example is a javelin head quite solidly embedded in the ivory, which is in the Museum of the Royal College of Surgeons.

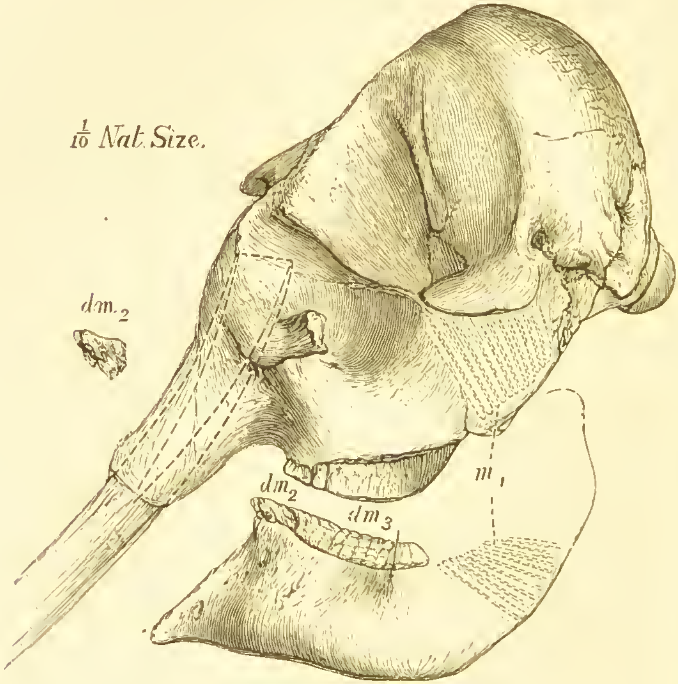
Six molar teeth are developed on each side of the jaw by the elephant, and, arguing from analogy, they are sometimes classified thus—milk molars $\frac{3}{3}$ true molars $\frac{3}{3}$; occasionally a rudimentary tooth in front brings up the number to seven on each side. But the peculiarity of their mode of succession renders such a classification merely arbitrary, so far as the elephant itself is concerned, and it depends upon analogy with the teeth of the mastodon. Though the elephant has, during the course of its life, twenty-four molars, they are not all in place, nor indeed are they all actually in existence at the same time. Only one whole tooth on each side, or portions of two (when the front one of the two is nearly worn out), are in use at the same time. After a tooth has been in use for some time, and is worn down, a new tooth comes up to take its place from behind it, and absorption in the old tooth being set up, it is shed off, and the new tooth pushes forward into its place (see fig. 156). Each successive tooth is of greater size than its predecessors; thus in the Indian elephant the first tooth having, on an average, four transverse plates; the second eight, the third twelve, the fourth twelve, the fifth sixteen, the sixth from twenty-four to twenty-seven. In the African elephant, in which the individual plates are much broader, they are fewer in number.

A reference to the accompanying figure will indicate how the succession takes place. The tooth in reserve occupies a position at an angle to that in use; as it moves forwards and (in the upper jaw) downwards its track forms almost the segment of a circle. Thus its anterior corner is the first to come into use, at a time when the position of the

whole tooth is still exceedingly oblique, and the greater part of it is still within the socket.

The teeth as first formed consist of detached plates of

FIG. 156 (1).



dentine coated with enamel, the tops of which are mammillated; these only coalesce after a considerable portion of their depth has been formed, and that portion of the tooth has been reached in which there is a common pulp cavity;

(1) Side view of skull of young Indian Elephant. The teeth in use are the second and third of the molars which displace one another from behind forwards; the anterior of these, corresponding to a milk molar in other animals, is nearly worn out; the residual fragment is separately represented on the left. The tusk, of which only a short piece can be shown, is indicated within the socket by dotted lines, by which also the form of the pulp cavity is mapped out.

here dentine is continuous from end to end of the tooth.

Just as the cusps of a human molar are separate when first calcified, so these exaggerated cusps or plates of an elephant's tooth are separate from one another till a great part of their length is completed, and they only coalesce when they reach the level of the common pulp chamber; in point of fact the elephant's tooth is mainly made up of its cusps, the remaining portion being insignificant.

Several of these detached plates, such as the one here figured, are to be found at the back of the largest teeth even at a time when the front corner has been erupted and has come into wear.

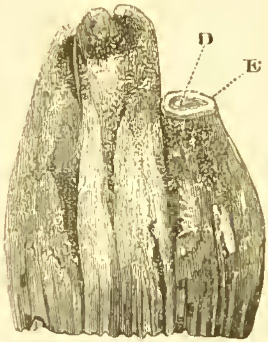
That the tooth is thus being built up only as it is required is of obvious advantage to the animal in diminishing the weight to be carried, and is also an economy of space.

The teeth when they begin to be erupted do not at once come into use over their whole surface, but they come forward in an oblique position, so that the front of the tooth has been in use for some time, and its plates have been considerably worn down, before the back of the tooth has become exposed at all. Nay, more, in the case of the larger molars the front of the tooth is actually in use at a time when its back is not yet completed.

In the elephant there is no vertical succession of teeth whatever; the manner of succession usual amongst mammals has in them given place to a succession from behind, the older teeth being pushed out forwards. Had the elephant always been as isolated a form as it now appears to be, it would have been very uncertain how its six molars should be classified. But it happens that proboscideans formerly existed in which this peculiar succession from behind was to be found, at the same time that the ordinary vertical succession was not quite lost, and amongst these creatures (the mastodons) we are able to say with certainty which of the

teeth are milk molars, which are premolars, and which are true molars. And as the mastodons pass by insensible gradations into the elephants, so that the line of demarcation between the two genera is an arbitrary one, we can tell

Fig. 157 ([1]).



which of the mastodon's teeth correspond to each one of the six molars of the elephant.

Mastodon.—In the later tertiary periods this genus, approximating in its dental and other characters to the true elephant, was widely distributed over the world. The dental formula is not quite the same for all the genus, for in some no premolars existed.

$$i\ \frac{1}{1}\ c\ \frac{0}{0}\ pm\ \frac{2}{2}\ \text{milk molars}\ \frac{3}{3}\ m\ \frac{3}{3}.$$

The upper incisors formed nearly straight tusks, seven or eight feet in length; the lower incisors also grew out horizontally from the front of the jaw, but in some species the lower tusks are rudimentary, are lost early, or are altogether

([1]) Isolated plate (= exaggerated cusp) of an Elephant's tooth, prior to its coalescence with neighbouring plates; at the top are seen its terminal mammillated processes, one of which has been cut off to show the central area of dentine, surrounded by enamel; at the base would be the open pulp cavity, not shown in the figure.

absent, thus more nearly approaching to the condition met with in the elephant.

The several molar teeth of the Mastodon increased in size from before backwards. The crowns were built up of deep and strongly pronounced transverse ridges, of which the last molar had the largest number. The apices of the ridges, before being at all worn, were divided up into several blunt nipple-like (mastoid) processes, upon which the enamel was thick and dense, but the cement was thin, so that the interspaces of the processes were not filled up level by the latter tissue, as in the elephant.

Very definite roots were formed to the molars, the wearing down of the teeth being met by the worn teeth being shed off altogether from the front of the series, whilst new teeth were added to the back. Thus, just as in the elephant, the whole number of teeth were not in place at one time. Not more than three were in use at one time, and by the time the last and largest molar was cut, there was but one tooth remaining in front of it, and even this was soon lost, the dentition thus being reduced to a single molar on each side.

As the succession of the molars in the Mastodon affords a clue to the nature of the grinders of the elephant, it is necessary to add a few words about it. Some Mastodons had three milk molars, of which the last two were vertically displaced by premolars, just as in most other mammals, but the first milk molar was not so replaced (Mastodon angustidens). There appear to have been Mastodons in which no vertical succession at all took place, *i.e.*, in which there were no premolars, and others in which there was but one.

No doubt can be entertained as to the homologies of the teeth, even in those Mastodons which are not known to have any vertical succession, because analogy with those other species in which the second and third molars, counted from the front, were vertically displaced by nearly functionless premolars, tells us that the three front molars are milk

molars. Now elephants develop six molar teeth on each side; the elephant is in the same case, quoad its molars, as the Mastodon Ohioticus, which had no vertical succession, so that we thus know the elephant's grinders to be

$$\text{dm}\ \frac{3}{3}\ \text{m}\ \frac{3}{3}.$$

Dr. Falconer mentions an elephant from the Sewalik Hills (E. planifrons) in which two rudimentary premolars, of no functional importance, actually existed, and so the determination of the elephant's working teeth as

$$\text{dm}\ \frac{3}{3}\ \text{m}\ \frac{3}{3}$$

rests not only upon analogy, but upon actual observation.

The Dinotherium, a large animal, not unlike the Sirenia in the character of its cranium, which was probably of aquatic habits, was remarkable for possessing large tusks, by analogy known to be incisors, in its lower jaw, none being present in the upper jaw. The tusks projected downwards at right angles with the body of the jaw and were curved backwards. The portion of jaw about the symphisis was deflected downwards, so as to afford an adequate implantation for these anomalous tusks.

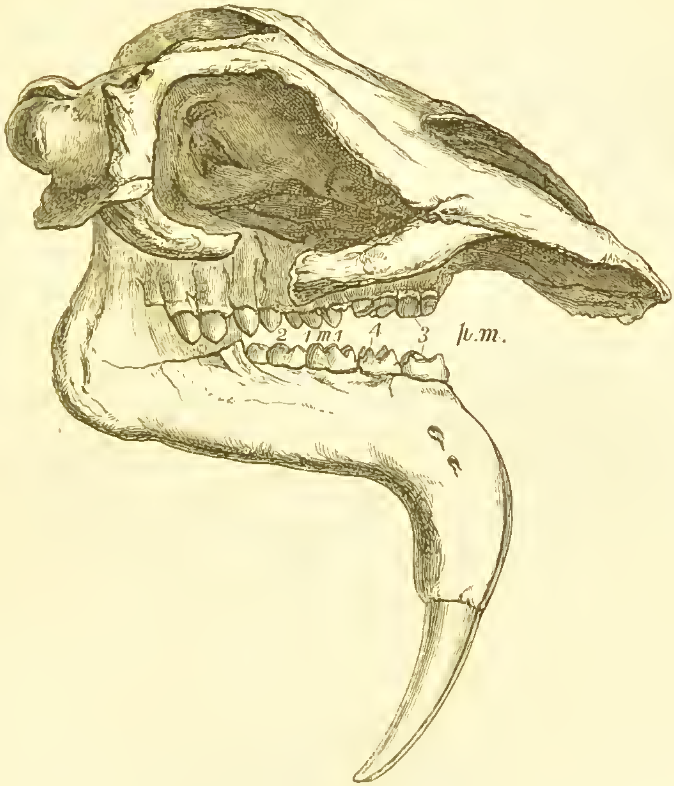
The dentine of these tusks does not, however, present the characteristic ivory pattern.

The Dinotherium was as large as an elephant, and the downward pointing tusks were about 2 feet in length; as, however, tusks of only half this length were found in some jaws of identical dimensions and in other respects similar, it is believed that the male Dinotherium had larger tusks than the female. The molar teeth, much like those of a tapir, need not detain us.

$$\text{i}\ \frac{0}{1}\ \text{c}\ \frac{0}{0}\ \text{pm}\ \frac{2}{2}\ \text{m}\ \frac{3}{3}.$$

The succession was vertical, as in other mammals, and it had dm $\frac{3}{3}$.

FIG. 158 (1).



But the Dinotherium, Mastodon, and Elephant, present us with a very instructive series of modifications in which we see how the excessively complex grinder of the Indian elephant was attained to by degrees.

The molar of the Dinotherium resembles that of a tapir somewhat; it has not any very great exaggeration of its cusps, and does not deviate very widely from the form of many other mammalian teeth.

(1) Skull of Dinotherium, after Owen.

The tooth of Mastodon has its cusps or ridges more numerous and more pronounced, as is seen in the accompanying figure.

Fig. 159 (1).

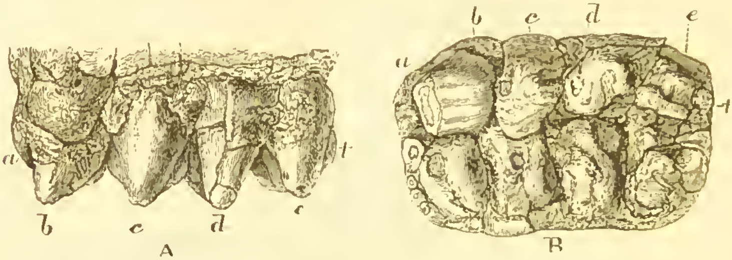


Fig. 160 (2).

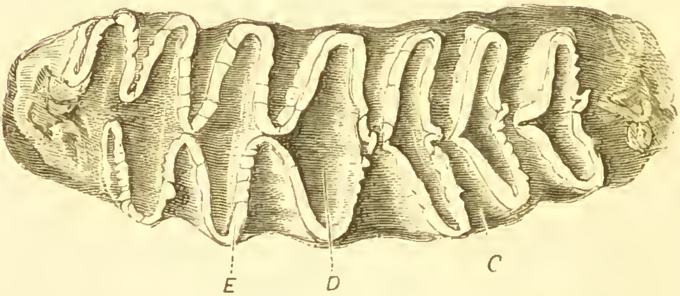
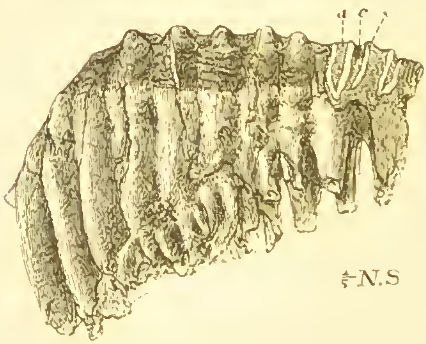


Fig. 161 (3).



(1) Molar tooth of Mastodon.

(2) Molar of African Elephant. *E.* Enamel. *D.* Dentine. *C.* Cementum.

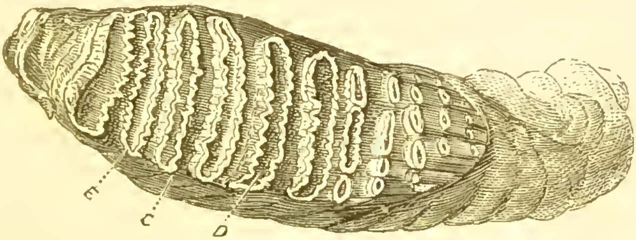
(3) Molar tooth of African Elephant, showing the form of its roots, &c. *a.* Dentine. *c.* Cementum. *e.* Enamel.

Other Mastodons have more numerous ridges upon the teeth, and the African elephant has as many as ten upon its last or larger molar, although in it the ridges are individually wide and strongly pronounced.

In the Indian elephant the ridges or plates are still more numerous, the roots very inconspicuous and the whole formed into a solid block by cementum.

The gradual increase in complexity in the "ridge formula"

Fig. 162 [1].



(or number of ridges in each tooth), of the molars, is well seen in the following table, from Prof. Flower's Hunterian lecture ("Nature," March 2, 1876); it is a corrected table taken from Dr. Falconer's "Palæontological Memoirs."

	Milk Molars.			True Molars.			Total.
	I.	II.	III.	I.	II.	III.	
Dinotherium giganteum . . .	1	2	3	3	2	2	13
Mastodon (Trilophodon) americanus	1	2	3	3	3	4	16
,, (Tetralophodon) arvernensis	2	3	4	4	4	5	22
,, (Pentalophodon) sivalensis	3	4	5	5	5	6	28
Elephas (Stegodon) insignis . . .	2	5	7	7	8	10	39
,, (Loxodon) africanus . .	3	6	7	7	8	10	41
,, ,, meridionalis . .	3	6	8	8	9	12	46
,, (Euelephas) antiquus . .	3	6	10	10	12	16	57
,, ,, primigenius . .	4	8	12	12	16	24	76
,, ,, indicus .	4	8	12	12	16	24	76

[1] Molar tooth of an Asiatic Elephant, showing the transverse plates of dentine bordered by enamel.

Some variability exists in the number of ridges, especially when they are very numerous, but the above may be taken as averages; and some species intermediate in the "ridge formula" have been since discovered; thus M. Pentelici and M. Andium bridge the distinction between Trilophodon and Tetralophodon, and Elephas melitensis comes between Loxodon and Euelephas (Flower).

It remains to describe, somewhat more in detail, the structure of an elephant's tooth, and this has been deferred till the last, because it can be the more easily understood when the manner of its origin has been mastered. In the Mastodon the molar consists of a crown with strong cusps standing apart, and with marked roots; in the African elephant that part which consists of cusps has become the greater bulk of the tooth, the roots are comparatively insignificant, and the interspaces of the cusps are filled up with cementum. The molar of the Indian elephant consists of a larger number of yet more elongated and flattened cusps, so that the greater part of the tooth is made up of these flattened plates, fused together with cementum, and so forming a strong and solid mass; the roots are comparatively inconspicuous.

When the tooth is a little worn each plate consists of an area of dentine surrounded by enamel. The interspaces of the series of plates are wholly filled up by cementum; the summits of each plate were originally mammillated, and divided up into more numerous blunt processes than the corresponding parts of the tooth of a Mastodon; when the tooth comes into use the rounded tips are soon worn off, and the grinding surface of the tooth then consists of narrow transverse bands of dentine, surrounded by enamel, and of cementum in their interspaces. The difference in hardness between these three tissues preserves a constant rough surface, owing to their unequal rate of wear. In their wild condition elephants eat trees with succulent juicy stems, and oftentimes grass torn up by the roots, from which they

roughly shake out the adherent earth. In confinement, the food containing less that is gritty, the teeth become polished by working against one another, but the rate of wear is insufficient to keep their surfaces rough ; for the softer cementum does not get worn down in the interspaces of the plates of dentine and enamel, but remains on a level with them.

The celebrated elephant "Jumbo" suffered from insufficient wear of his teeth, so that the earlier ones being insufficiently worn were not got rid of at the proper time, and interfered with the normal development of their successors.

Great though the size of the Proboscideans be, they have some points of affinity with the Rodents in the great development of the incisors, the vacant interval between these and the molar teeth, and, as was pointed out by the late Professor Rolleston, the enamel of the elephant's molar having, in its inner portions, a pattern produced by the decussation of the prisms, which is very similar to that described by my father as characteristic of all the Rodents save the Leporidæ (Hares), and Hystricidæ (Porcupines).

THE TEETH OF UNGULATA.

This is a group of animals of which a vast number of forms are extinct, and are only imperfectly known to us.

Recent discoveries, especially those of Professor Marsh in the Mauvaises Terres of Wyoming, have brought to light a very large number of strange and highly interesting forms, which have broken down the old classification of Ungulates into the Artiodactyle and Perissodactyle Ungulates, and have brought within it, by means of links, to a certain extent, Hyracoidea and Proboscidea.

Nowadays, provisionally, they may be grouped into Ungulata Vera and Subungulata.

The Ungulata Vera comprise—

(i.) Artiodactyles, or even-toed Ungulata	Hippopotamus, Pigs, Anoplotherium, Cows, Sheep, Deer, and other Ruminants.
(ii.) Perissodactyles, or Ungulata with an odd number of toes	Horses, Tapirs, Rhinoceros, Palæotherium.

The distinction between the two groups is strongly marked, if living animals alone be considered; but, as Professor Huxley has pointed out, increasing knowledge of fossil forms has broken down the line of demarcation.

Then we have an ill-defined group of—

Ungulata Polydactyla or Subungulata, comprising	Hyracoidea, Proboscidea, and Amblypoda, and perhaps others.

The Amblypoda comprise a number of extinct animals of huge size, as big as elephants. Prof. Cope includes in it Prof. Marsh's order Dinocerata, and to it may perhaps be referred several forms whose affinities are very puzzling, such as Toxodon.

But fortunately it is not necessary in an elementary work on Odontology to do more than present the descriptions of the several creatures somewhere near their right places, and so the increasing difficulties of the classification of the Ungulata need not be discussed.

Of Eocene Ungulata it may be said that almost all possessed the full mammalian dentition, *i.e.*

$$i\ \frac{3}{3}\ c\ \frac{1}{1}\ pm\ \frac{4}{4}\ m\ \frac{3}{3} = 44$$

and a few had more.

Moreover as we look at the patterns of the molar teeth, we find them far more simple, trituberculate or quadrituberculate crowns being the rule. Many of them have five toes, and were otherwise less specialised than modern forms. Ungulates mostly have a well developed milk dentition, which in the case of modern domesticated animals remain in use for a long time.

The Teeth of Perissodactyle Ungulates.—Perissodactyle (odd-toed) Ungulates are far less numerous than the even-toed section, and amongst recent animals only comprise the Horse, the Rhinoceros, the Tapir and their allies. Their premolars, or at least the last three of them, are equally

complex in pattern with the true molars; and canines, tusk-like but not very large, are of frequent occurrence. The lower molars of almost all perissodactyles have a characteristic form, their grinding surfaces being made up of two crescentic ridges.

The ungulate animals are all possessed of molar teeth, which are kept in an efficient state of roughness by the enamel dipping deeply into the crowns; by the cusps, in fact, being of very great depth. It consequently happens that after the immediate apex is worn away, the flattened working face of the tooth is mapped out into definite patterns, which, on account of the light thus thrown upon fossil remains, often consisting of little else than the teeth, have been studied with great care. The result has been to establish a general community of type, so that, dissimilar as they at first sight appear, it is possible to derive all, or almost all, the configurations of their crowns from one or two comparatively simple patterns. But odontologists are not yet agreed, or rather do not yet know enough of the vast number of extinct Ungulates which there is reason to believe once existed (of which many have lately been discovered) to decide with certainty what the parent pattern was.

The patterns of the molars have been made use of to divide them into the following groups:

(i.) Bilophiodont, *i.e.* two ridged, *e.g.* the Tapir.

(ii.) Molars (lower) bicrescentic, *e.g.* Rhinoceros.

(iii.) Lower molars bicrescentic, with the addition of inner lobes or columns, *e.g.*, Horse.

The Tapir is interesting as appearing in Miocene strata and remaining practically unchanged till the present time, it being thus the oldest existing genus of mammals (Flower).

Tapir.—The dental formula is

$$i\,\frac{3}{3}\;c\,\frac{1}{1}\;p\,\frac{4}{3}\;m\,\frac{3}{3}.$$

In a brief survey, like that to which the present work is necessarily confined, it will suffice to mention that there is no great peculiarity about the incisors or the canines, save that the third upper incisor is larger than the canine, and opposes the lower canine which ranges with the lower incisors;

Fig. 163 [1].

behind the canine comes an interval, after which come the premolars and molars, which are interesting, as being of simpler pattern than those of most Ungulates, and it will be necessary to very briefly allude to the various patterns characteristic of ungulate teeth, with a view of showing how they may have been derived the one from the other.

The first upper premolar is triangular, one of its cusps being suppressed, but the rest of them are squarish and resemble true molars.

In the Tapir four cusps are traceable, but ridges uniting the two anterior and the two posterior cusps are strongly developed, at the cost of the antero-posterior depression, *i.e.*, of one of the arms of the cross which separate the four cusps in other quadricuspid molars. There is therefore only a deep transverse fissure (hence it is called a bilophiodont tooth), and the quadricuspid form is disguised. A low wall on the outside of the tooth connects the two ridges.

In Rhinoceros the two external cusps are united by a longitudinal ridge, possibly the cingulum, and the transverse

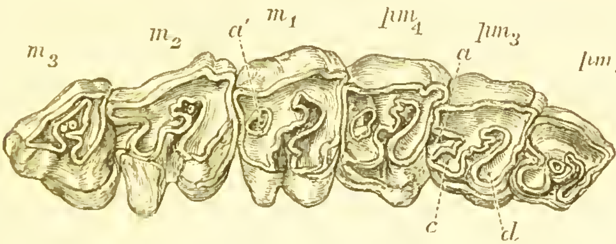
(1) Grinding surface of tooth of Tapir.

ridges become oblique; consequently the valley between the ridges *c* and *d* is also oblique in direction, and a second valley "*a*" behind the posterior ridge is introduced (Fig. 164).

The simplicity of the pattern is also departed from by the margins of the ridges, and therefore the boundaries of the depressions, being waved and irregular.

The lower molars of the Rhinoceros are made up of two crescentic ridges, one in front of the other, with the hollows turned inwards. It is less obvious how this pattern is

FIG. 164 (1).



derived from that of the Tapir, but it may be that the transverse ridges of the Tapir type of tooth may have become curved and crescentic, so that the original outer edge of the posterior ridge abuts against the back and the exterior of the ridge in front of it. The valleys between the processes of enamel and dentine of the tooth of the Rhinoceros, termed "sinuses," are not filled up solidly with cementum.

The Palæotherium type of tooth may be said to be arrived at by the outer wall becoming zigzag, being bent inwards opposite to the cusps, and outwards at the corners of the tooth and opposite to the interspaces between the cusps. The more complex pattern which characterises

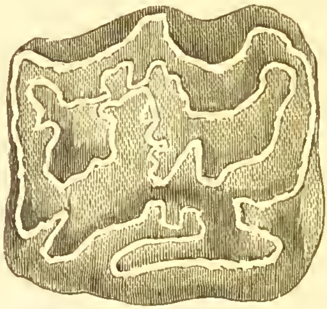
(1) Grinding surfaces of upper molar series of a Rhinoceros. *a.* Posterior sinus, which at *a* has become an island. *c.* Posterior ridge. *d.* Anterior ridge.

the molar of the Horse may be derived from a further modification of the Rhinoceros molar.

To use the words of Professor Huxley: "Deepen the valley, increase the curvature of the (outer) wall and laminæ (transverse ridges), give the latter a more directly backward slope; cause them to develop accessory ridges and pillars; and the upper molar of the Tapir will pass through the structure of that of the Rhinoceros to that of the Horse."

By a further increase in the obliquity of the ridges and

FIG. 165 (1).



in their curvature (*c* and *d*), they become parallel to the external or antero-posterior ridge (wall), and bend round until they again touch it, thus arching round and completely encircling the sinuses (*a* and the space between *c* and *d*) in the Rhinoceros tooth. In this way the unsymmetrical pattern of the Rhinoceros tooth may be supposed to become transformed into the comparatively symmetrical one of the Horse or of the ruminant.

The outer ridge or wall is in the upper molar of the horse doubly bent, the concavities looking outwards. The transverse ridges start inwards from its anterior end and from its middle, and they curve backwards as they go to such an extent as to include crescentic spaces (between themselves and the outer wall). To this we must add a vertical pillar,

(1) Molar tooth of Horse, showing the characteristic pattern of its grinding surface.

which is slightly connected with the posterior end of each crescentic edge (this pillar is in Hipparion quite detached).

The lower molars of the horse present the double crescent, just like those of the rhinoceros, save that vertical pillars are attached to the posterior end of each crescent, thus slightly complicating the pattern of the worn surface. The interspaces of the ridges and pillar are in the horse solidly filled in with cementum. The extinct ancestors of the horse are now, however, pretty well known, thanks to the researches particularly of Prof. Marsh; starting with the Eohippus, no larger than a fox, with four well-developed toes and a rudiment of the fifth (forefoot), through the Eocene Orohippus (4-toed), the Miocene Mesohippus as large as a sheep (3-toed, with rudimentary splint), the Upper Miocene Miohippus (3-toed), the Lower Pliocene Protohippus, as large as an ass (3-toed, but only the middle one reaching the ground), which was like the European Hipparion, and the Pliocene Pliohippus, which has lost the small hooflets, whilst in the Upper Pliocene the true Equus first appears.

Eohippus had forty-four teeth, the molars being quite distinct from the premolars, with short crowns and roots;[1] in Orohippus the last premolar is like the true molars, while in Mesohippus two premolars are like the true molars.

The other characters of the teeth are shown in the diagram better than they can be conveyed in words.

If we had specimens of most of the Ungulates which ever lived, there would be no doubt as to the relationship of the various patterns: as it is, we are embarrassed by the lack of the material, which leaves gaps too great to bridge over without some amount of speculation. As it is, Professor Flower divides the principal varieties of ungulate molars (Phil. Trans., 1874) into three:—

(i.) That in which the outer wall is feebly developed,

(1) Ancient deer also had short crowns to their molar teeth.

Fig. 166 (1).

RECENT.
Equus.

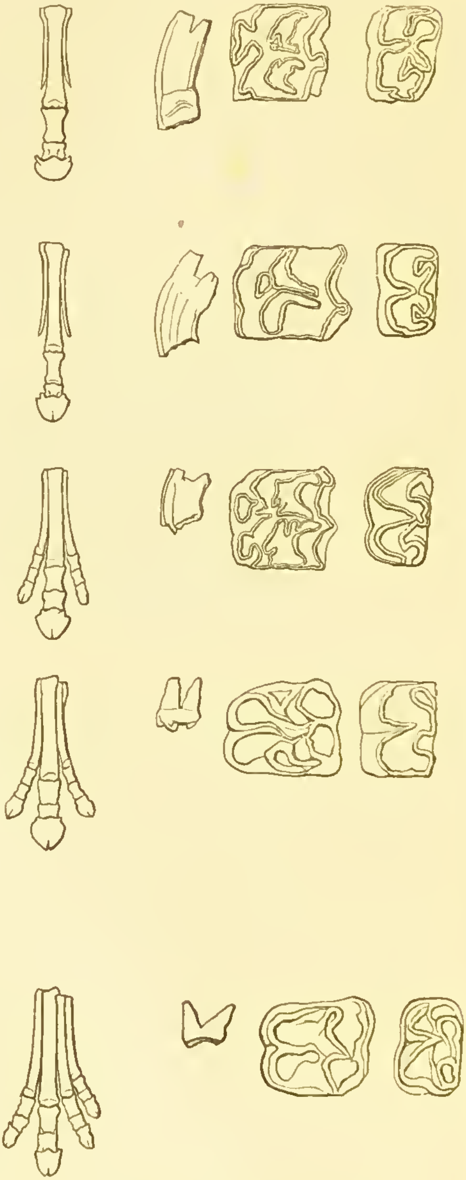
PLIOCENE.
Pliohippus.

Protohippus
(*Hipparion*).

MIOCENE.
Miohippus
(*Anchitherium*).

Mesohippus.

EOCENE.
Orohippus.



(1) Ancestry of the Horse. After Marsh.
The Forefoot and surfaces of upper and lower molars.

and transverse ridges become the prominent features, as in the tapir.

(ii.) That in which the outer wall is greatly developed and more or less smooth, the transverse ridges being oblique, as in the rhinoceros.

(iii.) That in which the outer surface and edge of the outer wall is zigzagged, or bicrescentic, as in the horse and palæotherium.

Equus.—The horse is furnished with the full mammalian number of teeth, the dental formula being—

$$i\,\frac{3}{3}\;c\,\frac{1}{1}\;p\,\frac{4}{4}\;m\,\frac{3}{3}.$$

The canines, however, are rudimentary in the female, whilst in the male they are well developed (in the gelding they are of the same size as in the entire horse); and the first premolar, which has no predecessor, is also rudimentary, and is

Fig. 167 (1).

lost early. A considerable interval exists between the incisors and the premolars and molars, which latter are very similar to one another, both in shape, size, and in the pattern of the grinding surface.

Mares occasionally have all four canines, but more commonly they have only the lower ones.

The incisors of the horse are large, strong teeth, set in close contact with one another; the teeth of the upper and lower jaws meet with an "edge to edge bite," an arrange-

(1) Apex of crown of an upper incisor of a Horse, not yet completely formed.

ment which, while it is eminently adapted for grazing, leads to great wearing down of the crowns. An incisor of a horse or other animal of the genus may be at once recognized by that peculiarity which is known as the "mark."

From the grinding surface of the crown there dips in a deep fold of enamel, forming a *cul de sac.* As this pit does not extend the whole depth of the crown, and the incisors

Fig. 168 (1).

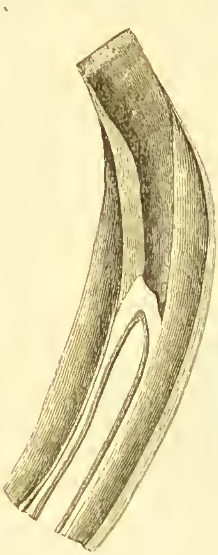
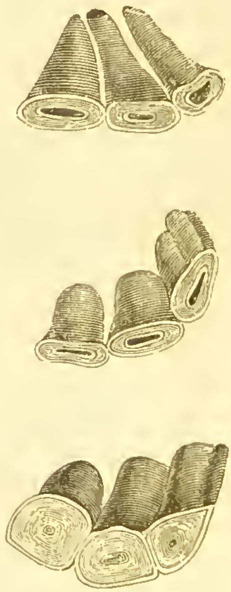


Fig. 169 (1.)



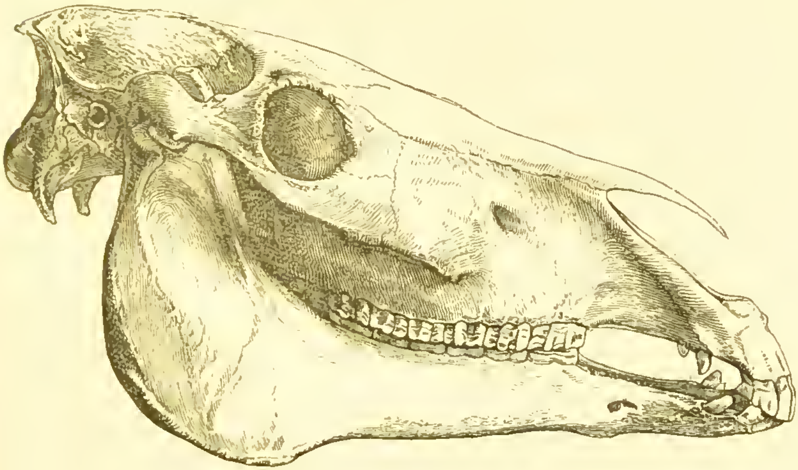
of a horse are submitted to severe wear, the fold eventually gets worn away entirely, and the worn surface of the dentine termed the "table" presents no great peculiarity. But as this wearing down of the crown takes place at something like a regular rate, horse dealers are enabled to judge of a horse's age by the appearance of the mark upon the different incisors. The "mark" exists in Hipparion, but not in the earlier progenitors of the horse.

(1) Incisors of the Horse, showing the marks at various stages of wear

A horse attains to its adult dentition very slowly. A foal is born with the two central incisors in each jaw; when nine weeks old it has four.

At $2\frac{1}{2}$ years the temporary central incisors are shed, at $3\frac{1}{2}$ the lateral, and at $4\frac{1}{2}$ the corner incisors, and at 5 years the horse is said to have a "full mouth." As the rate of wear

Fig. 170 [1].



is equal the mark gets worn out sooner upon the central incisors, and last upon the corner teeth.

At six the age is judged of chiefly by the wear of the corner teeth, as the cavity in centrals is nearly worn out, and the "table" nearly complete on the corner teeth. At the eighth year the central table is rather triangular, while from 8 to 10 years the small circle remains on centrals, and a round ring of enamel on corner teeth.

After 12 years the mark has wholly gone from centrals, and there is no certainty as to age.

[1] Side view of the dentition of a Stallion. At a short interval behind the incisors are seen the canines; then, after a considerable interval, the premolar and molar series.

After the "mark" is worn away the centre of the tooth is marked by a difference of colour, due to the presence of secondary dentine, into which the remains of the pulp has been converted.

While in the normal dentition the horse has only three premolars, yet a fourth, sometimes called wolf's-tooth, is present at the front of the row, a remnant of the fuller dentition of Palæotherium and Hipparion.

The molars of the horse are remarkable for their great length; they do not grow from persistent pulps, but nevertheless they do go on growing until a great length of crown of uniform diameter is made, subsequently to which the short and irregular roots are formed. As the upper working surface of the crown becomes worn, the tooth rises bodily in its socket, and when by an accident its antagonist has been lost, it rises far above the level of its neighbours. This elevation of the tooth takes place quite independently of growth from a persistent pulp, and, in fact, happens after the formation of its roots.

The pattern of the horse's molar has been already described; it should be added that the last molar differs from the rest in its posterior moiety being less developed than in the other teeth.

As each ridge and each pillar of the tooth consists of dentine bordered by enamel, and the arrangement of the ridges and pillars is complex; as, moreover, cementum fills up the interspaces, it will be obvious that an efficient rough grinding surface will be preserved by the unequal wear of the several tissues.

When a bit is put into a horse's mouth it rests in the interval, or diastema, which exists between the incisors and the commencement of the molar series, and the great convenience of the existence of such a space has led many authors to assume that the horse was moulded in accordance with man's special requirements, so that it might be suited for its subserviency to his wants.

But the wide diastema appeared in the remote ancestors of the horse long ages before man's appearance on the earth, and the advocates of this theory of design would, as Professor Huxley suggests, have to tell us what manner of animal rode the Hipparion.

The milk teeth of all the Ungulata are very complete, and are retained late; they resemble the permanent teeth in general character, but the canines of the horse, as might have been expected, their greater development in the male being a sexual character, are rudimentary in the milk dentition.

To the Perissodactyle Ungulates which are specially interesting on account of their dentition, must be added Homalodontotherium, a tertiary mammal, the remains of which were described by Professor Flower (Phil. Trans., 1874).

It had highly generalised characters; its teeth were arranged without any diastema, and the transition in form from the front to the back of the mouth was exceedingly gradual, so that no tooth differed much from those on either side of it. Taking the pattern of its molar teeth alone into account, it would have been without hesitation declared to be very nearly allied to rhinoceros, on which type they are formed, but the resemblance fails in the canine and incisor region, and it must be considered to be one of those generalised types related to rhinoceros, to Hyracodon and perhaps connecting them with such aberrant forms as Toxodon.

The largest of Perissodactyles equalled the elephant in size, and have been named by Prof. Marsh Brontotheridæ. The dental formula was

$$i\ \frac{2}{2}\ c\ \frac{1}{1}\ pm\ \frac{4}{3}\ m\ \frac{3}{3}.$$

The incisors were small and sometimes deciduous, and the canines short and stout, the lower being the more conspicuous

owing to its being separated by a slight diastema from the premolars, which is not the case in the upper jaw.

The premolars in both jaws increase in size from before backwards, and do not differ from the molars next them. In the lower jaw the premolars and molars all consist of two crescents, save the last, which have three crescentic cusps. The molar teeth stand apart from those of any recent perissodactyles in their huge size, the squarish last upper molar, for example, measuring four inches antero-posteriorly and more than three transversely (Prof. Marsh, American Journal of Science and Arts, 1876).

THE TEETH OF ARTIODACTYLE UNGULATA.

Artiodactyle, or even-toed Ungulata, comprise pigs, hippopotami, camels, sheep, oxen, &c., amongst living animals.

They are grouped into

(i.) Bunodonts, or Suina, comprising Pigs and Hippopotami.

(ii.) Selenodonts, comprising Anoplotheridæ and the ruminants.

(*a.*) The Tylopoda or Camels.

(*b.*) The Tragulidæ. Small deer of S. Asia. Chevrotains, which are somewhat intermediate between the Suidæ and the deer.

(*c.*) Pecora, or sheep, oxen, and deer.

The primitive Artiodactyla all had forty-four teeth of brachyodont type: in later geological times they became long-toothed (hypsodont) like recent sheep and oxen.

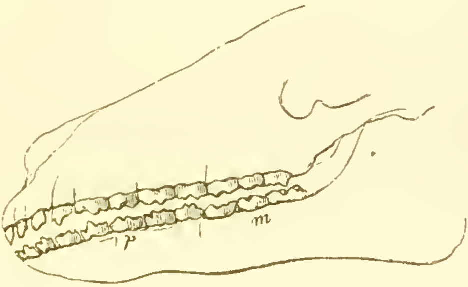
Anoplotheridæ are an extinct (Eocene and Miocene) family, of somewhat specialised character, and apparently not on the direct line of descent of any modern forms.

Anoplotherium is a genus of interest to the odontologist because it possessed the full typical mammalian dentition,

as far as the number of the teeth went; the teeth were of nearly uniform height, none strongly differentiated from those nearest to them; and they were set in close contiguity with one another, so that there was no "diastema."

The lower molar teeth of the Anoplotherium are built up on the same type as those of the Rhinoceros, and present the same double crescent: the upper molars are also referable to the same fundamental forms, though the difference is greater. The laminæ (transverse ridges) oblique in the

Fig. 171 [1].



Rhinoceros, are in Anoplotherium still more oblique, so that they become more nearly parallel with the outer wall, and an accessory pillar is developed at the inside of the anterior laminæ.

Not very widely removed from Anoplotherium is Oreodon, an Ungulate of eocene age.

Like a good many tertiary Ungulates (both artiodactyle and perissodactyle) it had the full typical number of teeth, forty-four; but its interest to the odontologist is enhanced by the co-existence of strongly marked canines with molars very much like those of ruminants, a group almost always devoid of canines.

In the upper jaw Oreodon had

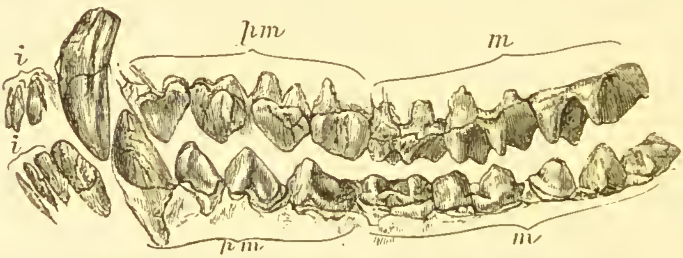
$$i\,\frac{3}{\;}\;c\,\frac{1}{\;}\;pm\,\frac{4}{\;}\;m\,\frac{3}{\;}$$

[1] Side view of the dentition of Anoplotherium (after Owen).

i.e., the typical number of each kind of teeth. But in the lower jaw the first *four* teeth are like incisors, and the tooth which is like a canine is not the tooth corresponding to the upper canine, but to the small upper first premolar.

This is a fair illustration of the fact that although in nature it is generally the same tooth which is modified to perform the function of a canine, it is not invariably the same; for here in the same animal are two different teeth in the upper and lower jaws thus respectively modified.

FIG. 172 (1).



And as they are different teeth, it happens that the upper (canine) closes in front of the lower.

There is reason to believe that there was some difference in the size of canines between the male and female Oreodon.

In Artiodactyle Ungulata the premolars differ markedly both in size and pattern from the true molars.

Of those Artiodactyle Ungulates which are not ruminants the common pig may be taken as an example.

The dental formula is i $\frac{3}{3}$ c $\frac{1}{1}$ p $\frac{3}{3}$ m $\frac{3}{3}$.

The position of the upper incisors is peculiar, the two central upper incisors, separated at their bases, being inclined towards one another so that their apices are in contact; the

(1) Upper and lower teeth of Oreodon Culbertsonii (after Leidy, Smithsonian Contributions, 1852).

third pair are widely separated from the inner two pairs of incisors. The lower incisors are straight, and are implanted in an almost horizontal position: in both upper and lower jaws the third or outermost incisors are much smaller than the others.

The lower incisors are peculiar in having upon their upper surfaces a strongly pronounced sharp longitudinal ridge of enamel, which gets obliterated by wear.

An interval separates the incisors from the canines, which latter are very much larger in the male than in the female, and in the wild boar than in the domesticated animal. Castration arrests the further development of the tusks; the peculiarities as to size and direction which characterise the tusks of the adult animal are not represented in the canines of the milk dentition, about which there is not much that is noteworthy, save that the young pig has dec. m $\frac{4}{4}$, of which the first remains in place till the permanent dentition is nearly complete, and then falls out without having any successor; or it may perhaps be regarded as a permanent tooth which has had no predecessor.

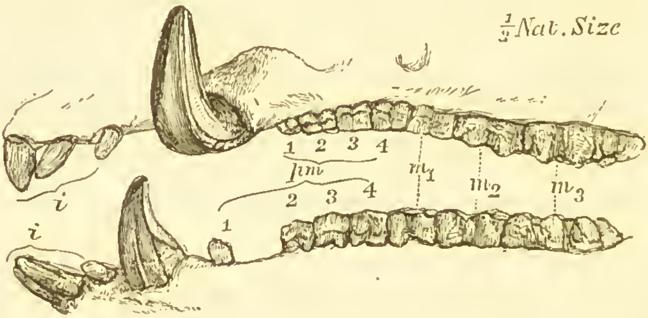
A similar condition as to early loss of the tooth immediately behind the canine obtains in the Dog and in the Hippopotamus, their dental formulæ being generally written p. $\frac{4}{4}$.

The form and direction of the canines are alike peculiar; the upper canine, which in its curvature describes more than a semicircle, leaves its socket in a nearly horizontal direction, with an inclination forwards and outwards. After rounding past the upper lip its terminal point is directed upwards and inwards. The enamel upon the lower surface of the tusk is deeply ribbed: it does not uniformly cover the tooth, but is disposed in three bands. The lower canines are more slender, of much greater length, and by wear become more sharply pointed than the upper ones: they

pass in front of the latter, and the worn faces of the two correspond.

The lower canine is in section triangular, one edge being directed forwards, and its sides being nearly flat. Enamel is confined to the internal and external anterior surfaces; the posterior surface, which plays against the upper canine, is devoid of enamel, and the tooth is kept constantly pointed by the obliquity with which its posterior surface is worn away. The tusks of a boar are most formidable weapons, and are

Fig. 173 (1).



capable of disembowelling a dog at a single stroke, but they are greatly exceeded by those of the African Wart-hog Phacochœrus), which attain to an immense size.

In the domestic races the tusks of the boars are much smaller than in the wild animal, and it is a curious fact that, in domestic races which have again become wild the tusks of the boars increase in size, at the same time that the bristles become more strongly pronounced. Mr. Darwin suggests that the renewed growth of the teeth may perhaps be accounted for on the principle of correlation of growth, external agencies acting upon the skin, and so indirectly influencing the teeth.

As in most Artiodactyles, the teeth of the molar series

(1) Upper and lower teeth of Wild Boar (Sus scrofa). In this specimen the tusks are not so largely developed as they sometimes may be seen to be.

increase in size from before backwards: thus the first premolar (?milk molar) has a simple wedge-shaped crown, and two roots; the second and third by transitional characters lead to the fourth premolar, which has a broad crown with two principal cusps, and has four roots.

The first true molar has four cusps divided from one another by a crucial depression; and the cingulum in front, and yet more markedly at the back, is elevated into a posterior transverse ridge. In the second molar the transverse ridge is more strongly developed, and the four cusps are themselves somewhat divided up into smaller accessory tubercles.

The last molar measures, from front to back, nearly twice as much as the second; and this great increase in size is referable to a great development of the part corresponding to the posterior ridge or cingulum of the second molar, which has become transformed into a great many subsidiary tubercles.

That such is a correct interpretation of its nature is indicated by our being able to trace the four principal cusps, though modified and not divided off, in the front part of the tooth, of which, however, they do not constitute more than a small part. Those Ungulates in which the surfaces of the molar teeth are covered by rounded or conical cusps, are termed "bunodonts," in contradistinction to those which present crescentic ridges on the masticating surface of their molars, and which go by the name of "selenodonts."

In the Wart-hog (Phacochœrus), the genus with very large canines, the disproportion between the last true molar and the other teeth is yet more striking.

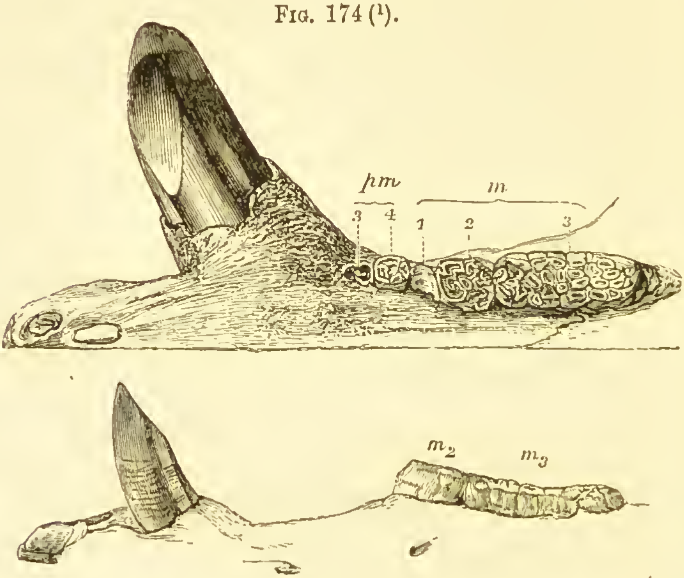
In antero-posterior extent the third molar equals the first and second true molars and the third and fourth premolars (the whole number of teeth of the molar series possessed by the animal) together.

When a little worn its surface presents about thirty islands of dentine, surrounded by rings of enamel, the interspaces and the exterior of the whole being occupied by cementum.

Of course, prior to the commencement of wear, each of these islands was an enamel-coated cusp.

The Wart-hog's dentition has, however, another instructive peculiarity; the first true molar is in place early, and becomes much worn down (this is true, in a less degree, of the common pig, and indeed of most Ungulata). Eventually it

FIG. 174 (1).



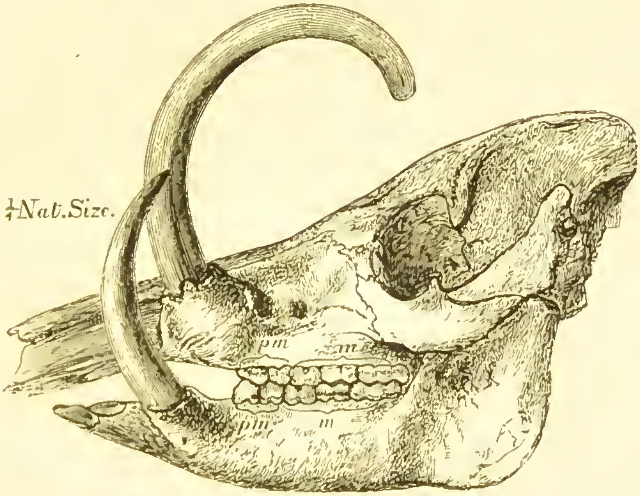
is actually shed; the same fate later befalls the third premolar and second true molar, so that the dentition in an aged specimen is reduced to the fourth premolar and the third true molar alone, and eventually to the last true molars alone. Thus, both in the great complexity of the back molars and the fact that the anterior teeth are worn out and then discarded, the Wart-hog affords a parallel to the anomalous dentition of the elephant.

(1) Upper and lower teeth of Phacochœrus. In the upper jaw, the last two premolars, and the much-worn first true molar remain. In the lower all have been shed off, save the last two true molars. From a specimen in the Museum of the Royal College of Surgeons.

As has already been noticed, the upper canines in the boar turn outwards and finally upwards, so as to pass outside the upper lip; this peculiarity in direction, yet more marked in Phacochœrus, attains its maximum in the Sus babirussa.

This creature, strictly confined to the Malay Archipelago, where it frequents woody places, has (in the male) the upper and lower canines developed to an enormous extent. The upper canines are turned upwards so abruptly that they

Fig. 175 ([1]).



pierce the upper lip, instead of passing outside it as in other Suidæ, preserve a nearly upright direction for some little distance, and then curve backwards, so that their points are directed almost towards the eyes.

The lower canines are less aberrant in direction and in shape, being somewhat triangular in section, but they also are of very great length, and pass upwards, far above the level

([1]) Skull of Sus babirussa (male). The upper incisors have been lost from the specimen figured: they are much like those of a pig.

of the snout; their points are also directed backwards, but have in addition an outward inclination. The canines are devoid of enamel, and grow from persistent pulps, a fact which sometimes has a disastrous result, for the tip of the tooth, occasionally taking a wrong direction, re-enters the head or the jaws of the animal.

Their length is very great; the animal is smaller than the domesticated pig, but its canines attain a length of eight or ten inches. Their use is a matter of conjecture; the position of the upper tusks has suggested the idea that they may serve as a protection to the creature's eyes, as it seeks its food, consisting of fallen fruits, amongst the brushwood. But were that the case the female also would probably have them, which is not the case, the upper canine being only about $\frac{3}{4}$ inch long, though it is everted and is beginning to turn upwards; the lower tooth is a little larger; and although in old animals they are often broken off, it is not certain that they are much employed in fighting. Its other teeth are in no respects remarkable.

Hippopotamus.—The dental characters, as well as others, indicate the affinity of the Hippopotamus to the Suidæ.

$$i\ \frac{2}{2}\ c\ \frac{1}{1}\ p\ \frac{4}{4}\ m\ \frac{3}{3}.$$

The incisors are tusk-like, and bear but little resemblance to those of most other mammalia; they are nearly cylindrical, bluntly pointed at their apices by the direction of wear, and this is in some measure determined by the partial distribution of the enamel, which is laid on in longitudinal bands in the upper teeth, but merely forms a terminal cap on the lower incisors.

The upper, standing widely apart, are implanted nearly vertically: the lower incisors, of which the median pair are exceedingly large, are implanted horizontally.

The canines are enormous teeth; the lower, as in the Hog,

are trihedral, and are kept pointed in the same manner; the upper canines are not so long, and the portion exposed above the gum is relatively short.

The incisors and canines are all alike teeth of persistent growth.

The premolars, of which the first is lost early (being, like the similar tooth in the pig, perhaps a milk molar) are smaller and simpler teeth built up on the same type as the true molars.

These latter, especially when worn, have a very characteristic double trefoil pattern; the four cusps, in the first instance, were separated by a deep longitudinal and a still deeper transverse groove; each cusp was, moreover, trilobed; the first result of wear is to bring out the appearance of four trefoils; next, when the longitudinal furrow is worn away, two four-lobed figures result; and finally all pattern becomes obliterated, and a plain field of dentine surrounded by enamel alone remains.

The teeth of the Hippopotamus are subject to a great amount of attrition, as is well shown by a specimen presented to the Museum of the Odontological Society, in which the molar teeth are all excessively worn. The Hippopotami use their incisors and canine tusks for the purpose of uprooting aquatic plants, of which their food mainly consists: the roots of these are of course mixed up with much sand, which wears down the teeth with great rapidity. The larger incisors and the canines are, and for centuries have been, articles of commerce, the ivory being of very dense substance and useful for the manufacture of small objects.

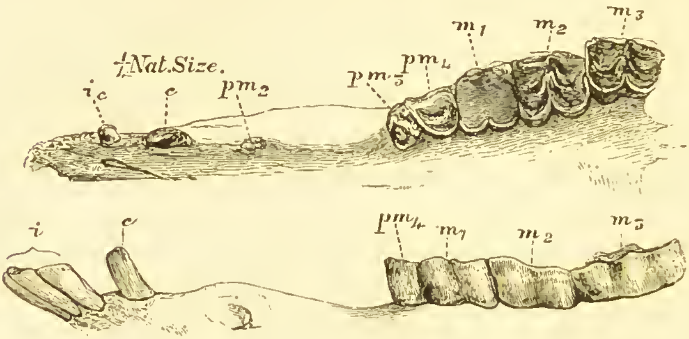
The remaining Selenodont Ungulates are divided into the Tylopoda (Camels), the Tragulina and Pecora.

The Camels have both upper incisors and canines, the dental formula being:—

$$i\,\frac{1}{3}\;c\,\frac{1}{1}\;p\,\frac{3}{2}\;m\,\frac{3}{3}.$$

The first two pairs of upper incisors are absent, but the third or outermost pairs are present, and are rather caniniform in shape. In quite young skulls six upper incisors are pre-

FIG. 176 ([1]).



sent, but the two inner pairs are lost very early. The canines are strong pointed teeth, and the lower canine

FIG. 177 ([2]).

stands well apart from the three incisors of the lower jaw, unlike the fourth tooth in front of the mandible of typical pecora (see Fig. 178).

The first premolars are absent altogether; the second premolars, following the canines after an interval, are pointed caniniform teeth. The third premolar is sometimes lost early, but the fourth persists.

The molars of the Camel are of the "Selenodont" type;

([1]) Upper and lower teeth of a Camel.
([2]) Selenodont molar of a deer.

their derivation from forms already alluded to will be sufficiently obvious to the reader who has mastered the descriptions, and their double crescentic crowns, may be taken as fair examples of simple ruminant patterns, accessory pillars, &c., being added in some of the other families.

The Tragulina or Chevrotains, sometimes called Pigmy Musk Deer, though somewhat intermediate between the Pigs and Deer, and zoologically distinct enough, do not differ in their dentition from the true ruminants, with which they may be noticed here.

The hollow-horned ruminants (sheep and oxen and antelopes), and likewise almost all the solid horned ruminants (deer) have the following dental formula :—

$$i\,\frac{0}{3}\;c\,\frac{0}{1}\;\text{or}\;c\,\frac{1}{1}\;p\,\frac{3}{3}\;m\,\frac{3}{3}.$$

The lower incisors are antagonised not by teeth, but by a dense gum which clothes the fore part of the upper jaw; if a sheep is watched as it feeds, it will be seen to grasp the blades of grass between the lower teeth and the gum, and then to tear them off by an abrupt movement of the head, as it would be impossible for it to, strictly speaking, bite it off.

The anomaly of the entire absence of upper incisors was held to have been diminished by the statement of Goodsir, who believed that uncalcified tooth germs were to be found in the fœtuses of many species. As this was precisely what might have been expected, it has since that time passed current as an established fact; but M. Pietkewickz, working in the laboratory of M. Ch. Robin, has absolutely denied the occurrence of even the earliest rudiments of tooth germs in this situation, after an examination of a series of fœtuses of the sheep and cow, ranging even from the earliest periods. (Journal d'Anatomie, par C. H.

Robin, 1873, p. 452.) Since meeting with this statement I have had no opportunity of verifying this matter myself.

Grouped with the six incisors of the lower jaw, and in no respect differing from them, rise the pair of teeth which are very arbitrarily termed "canines." As I cannot attempt to do more in these pages than give the most bare outline of generally well-known facts, I have retained the usual dental formula, $i\,\frac{0}{3}\;c\,\frac{0}{1}$; though under protest, as I do not consider the "canine" to have any such distinct existence as would justify our calling a tooth which is so obviously referable to the incisors by any distinctive name.

Although the absence of upper canine teeth is a very general characteristic of ruminants, rudimentary canines exist in some deer, and I am indebted to the kindness of Sir Victor Brooke, a high authority upon the *Cervidæ*, for the following:—

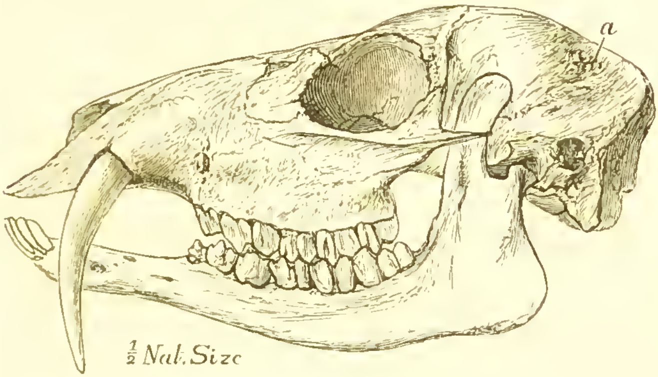
"The upper canines are present in both sexes in all the species of *Cervidæ*, with the exception of Alces, Rangifer, Dama, some smaller species of Rusa, Axis, Capreolus, Cariacus, Blastocerus, Coassus, and Pudu. The upper canines, when present, are with the notable exception of Moschus, Elaphodus, Cervulus, and Hydropotes, small laterally compressed rudimentary teeth. Their crowns are in about the same stage of reduction as the crowns of horses' canines, but their roots are relatively much more reduced." Hence they are often lost in dried skulls, and it has generally been supposed that but few deer possessed canines at all.

The hornless musk deer possesses upper canines of most formidable dimensions, while the female has very small subcylindrical canines.

The male pigmy musk deer (Tragulus) has large canines of persistent growth, the female small canines with closed roots.

The Indian Muntjac deer (Cervulus) has somewhat small horns, which are perched upon persistent bony pedicles, and it has upper canines which are curved outwards from beneath the upper lip, much as are the tusks of a boar; they do not, however, grow from persistent pulps, and are absent in the female.

FIG. 178 (1).



Cuvier first pointed out that there was a relation between the presence of horns and the absence of canine teeth; the latter, serving as weapons for sexual combat solely, and being, probably, in no other way of service to the animal, are not required by an animal provided with powerful antlers or horns, whereas the absolutely hornless musk deer would be totally unprovided with weapons of offence were it not for his canines. To the musk deer and the muntjac must be added Swinhoe's water deer, Hydropotes inermis, which has canines shorter and stouter than Moschus, and Michie's deer, Elaphodus cephalopus, another small hornless species, of which the males are furnished with formidable canine teeth, which are not so long as those of Moschus, but are flattened from side to side, and are very strong.

(1) Cranium of male Musk deer (Moschus moschiferus).

Although, with the foregoing exceptions, all the deer, oxen, sheep, antelopes, and the giraffe, animals constituting the greater number of the "Ruminantia," are without canine teeth, yet in the Camelidæ, tusk-like canines are met with.

It is a character of the Artiodactyle Ungulata that the premolar teeth are of decidedly simpler form than the molars; in the ruminants the premolars may be said each to roughly correspond to one half of a true molar, and the premolars and molars form a continuous series.

In all true Ruminants the last true molar of the lower jaw has a third lobe (1), and the line of the outer surface of the row of teeth is rendered irregular by the anterior edge of each tooth projecting outwards slightly more than the posterior border of the one in front of it. And the deviations in the patterns of the surfaces of the molar teeth are so constant and so characteristic that, although the common ruminant pattern is preserved in all, it is often possible to refer an individual tooth to its right genus.

The Ruminants all have a well-developed milk dentition, which serves the animal for a long time, indeed until after it has attained to its adult dimensions; thus a sheep has not completed the changing of its teeth till the fifth year, and a calf till the fourth year. But the first permanent molar is in them, as in so many other animals, the first of the permanent set to be cut, and comes up in its place at the sixth month (in the lamb), and hence has a long period of wear before any of the other second teeth are cut. Consequently the first permanent molar is, as is seen in Fig. 176, invariably worn down to a much greater extent than the other permanent teeth; in the specimen figured it has been worn down below the inflections of enamel, so that it

(1) Sir Victor Brooke informs me that Neotragus hemprichii, a small Abyssinian antelope, has only two lobes to the third lower molar.

has lost its roughened grinding surface, and is reduced to a smooth area of dentine.

Not much is known of the structure of the dental tissues of the Ungulata calling for mention in an elementary work. The thick cement of the crown of the teeth of the Horse, and indeed of most of the group which possess thick cement, contains many "encapsuled lacunæ," and is developed from a distinct cement organ of cartilaginous consistence.

AMBLYPODA.

The Polydactyle Ungulates form an ill-defined group, to which Hyrax and Proboscidea may be referred, as well as a number of extinct forms, mostly American, the exact affinities of which remain uncertain.

TOXODONTIA.

The existing ungulate animals form only a small proportion of those once peopling the earth, and many extinct forms have been discovered, which while forming affinities with the Ungulata, can yet hardly be classified under any existing order. For example, Toxodon, a creature equalling the Hippopotamus in size, which was discovered by Mr. Darwin in late tertiary deposits of South America, has a dentition recalling in some respects the Bruta, in others the Rodents.

Its dental formula was

$$i\,\frac{2}{2}\;c\,\frac{0}{1}\;p\,\frac{4}{3}\;m\,\frac{3}{3}.$$

It possessed in the upper jaw two pairs of incisors, the

median pair small, the outer exceedingly large, with persistent pulps, and long curved sockets extending back to the region of the molars, just as in existing Rodents.

In the lower jaw there were three pairs of incisors, subequal in size, and growing from persistent pulps; they resemble the incisors of Rodents in having a partial investment with enamel, but differ from them in being prismatic in section, and in having the enamel disposed on two sides of the prism.

The molars were also very remarkable; they grew from persistent pulps, and had curved sockets, but the curvature of these was in the reverse direction to that which obtains in Rodents, *i.e.*, the convexity was outwards, and the apices of their roots almost met in the middle line of the palate; it was this peculiarity that suggested the name.

Another peculiarity in the molar teeth, in which they stand quite alone, is that, like incisors, they have a partial investment with enamel; those referred to the premolar series having it confined to their outer surfaces, while the three back teeth of the molar series had a plate also laid on to their inner surfaces; there were seven back teeth above, and six below.

In the interval between the incisor and molar series canines have been found in the lower jaw; they were sharp edged, and had a partial distribution of enamel over their surface. In an upper jaw alveoli for canines were found, but the teeth themselves are not known.

Another animal from the same locality (Mesotherium) had somewhat similar characters, though it was not nearly so large: it had

$$\text{i}\,\frac{1}{2}\;\text{c}\,\frac{0}{0}\;\text{pm}\,\frac{2}{1}\;\text{m}\,\frac{3}{3},$$

the incisors (of persistent growth) standing apart from the premolar and molar series just as in the Rodents.

DINOCERATA.

In the same region which yielded the toothed birds (Eocene formations of Wyoming), the remains of many huge animals have been discovered, for which new orders have been proposed by Prof. Marsh (American Journal of Science and Art, 1876), it being impossible to classify them under any existing order. The Dinocerata were creatures nearly as large as elephants, and presenting some sort of resemblance to them in general form; they were remarkable for the relative smallness of their brains, which could apparently have been drawn through the canal of the vertebral column. They present points of resemblance to the Perissodactyle Ungulata, and also to the Proboscidea, to which they were at first referred, though their affinities are rather with the former.

The dental formula was

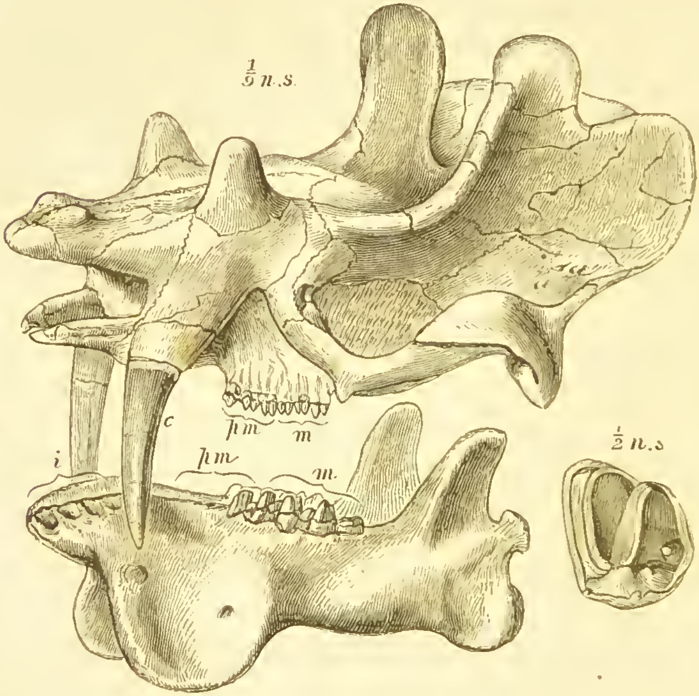
$$i\,\frac{0}{3}\;c\,\frac{1}{1}\;prm\,\frac{3}{3}\;m\,\frac{3}{3}.$$

In Prof. Marsh's words, "The superior canines are long, decurved, trenchant tusks. They are covered with enamel, and their fangs extend upwards into the base of the maxillary horn-core. There is some evidence that these tusks were smaller in the females. Behind the canines there is a moderate diastema. The molar teeth are very small. The crowns of the superior molars are formed of two transverse crests, separated externally, and meeting at their inner extremity. The first true molar is smaller in this specimen than the two preceding premolars. The last upper molar is much the largest of the series.

"The lower jaw in Dinoceras is as remarkable as the skull. Its most peculiar features are the posterior direction of the condyles, hitherto unknown in Ungulata, and a massive decurved process on each ramus extending downward and outward below the diastema.

"The position of the condyles was necessitated by the long upper tusks, as, with the ordinary ungulate artieulation, the mouth could not have been fully opened. The low position of the eondyle, but little above the line of the teeth, is also a noteworthy eharaeter. The long pendant proeesses were

Fig. 179 (1).



apparently to proteet the tusks, whieh otherwise would be very liable to be broken. Indieations of similar proeesses are seen in Smilodon and other Carnivores with long upper eanines. With the exeeption of these proeesses the lower jaw of Dinoeeras is small and slender. The symphysis is eompletely ossified. The six ineisors were eontiguous, and all directed well forward. Just behind these, and not

(1) Upper and lower jaws of Dinoceras (Marsh).

separated from them, were the small canines, which had a similar direction. The crowns of the large molars have transverse crests, and the last of the series is the largest."

It would appear possible that the eminences shown in the figure, and spoken of as "maxillary horn-cores," may be merely the extended sockets of the teeth, which would otherwise have had an implantation inadequate to their length; they are, however, described as solid, except at their bases, where they are perforated for the fang of the canine tusk, which would look as though they were truly horn-cores; moreover the Brontotheridæ had horn-cores equally peculiar in position (*i.e.*, on the maxillary bones).

Tinoceras, another genus, had a very long and slender canine, also protected, when the mouth was closed, by a downward prolongation of the lower jaw as in Dinoceras.

TILLODONTIA.

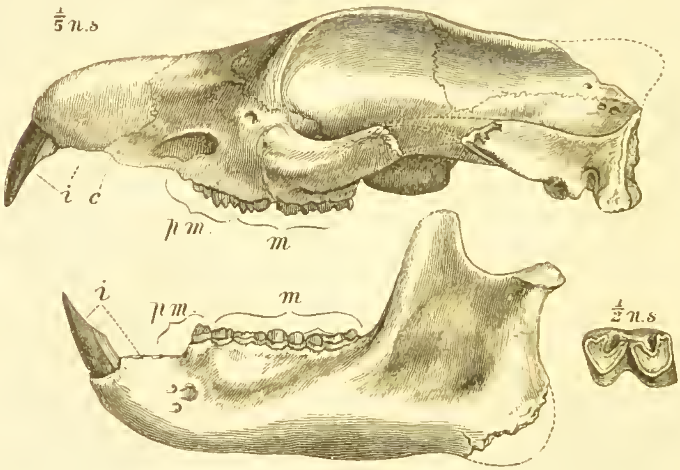
This, yet another new order, comprising several genera, has been proposed by Prof. Marsh for Wyoming fossil remains, to receive forms which, though not amongst the biggest, are "amongst the most remarkable yet discovered in American strata, and seem to combine characters of several distinct groups; viz., Carnivora, Ungulata, and Rodentia." In Tillotherium, Marsh, the type of the order, the skull has the same general form as in the bear, but in its structure resembles that of the Ungulata. Its molar teeth are of the Ungulate type, the canines are small, and in each jaw there is a pair of large scalpriform incisors, faced with enamel and growing from persistent pulps, as in the Rodents. The second pair of incisors are small, and have not persistent pulps. The adult dentition is as follows—

$$i\,\frac{2}{2}\;c\,\frac{1}{1}\;prm\,\frac{3}{2}\;m\,\frac{3}{3}.$$

"There are two distinct families, *Tillotheridæ* (perhaps identical with *Anchippodontidæ*), in which the large incisors grew from persistent pulps, while the molars had roots; and the *Stylinodontidæ*, in which all the teeth have persistent pulps."

One genus (Dryptodon), known only by the lower jaw, had six teeth, described as "clearly incisors," the two inner pairs

FIG. 180 (1).



of which are small and cylindrical, the outer of enormous size, faced in front only with enamel, and with persistent pulps carried back under the premolars.

Whilst Prof. Flower endorses Prof. Marsh's view that Tillodonts have Ungulate affinities and resemblances to Rodents also, this is disputed by Mr. Dall (Amer. Syst. Dental Surgery, Art. Teeth of Vertebrates), who says that he fails to discover any traces of Ungulate relationship, and he prefers to refer them to those generalised forms with Insectivorous affinities which Prof. Cope groups as Bunotheria. The adaptive character of incisors faced with enamel and of

(1) Upper and lower jaws of Tillotherium (Marsh).

persistent growth he would appear to consider as not going far towards establishing more than a superficial resemblance to Rodentia.

The pattern of its molar teeth is closely similar to that of Esthonyx (Cope), an Eocene mammal with a dentition resembling that of a gigantic Shrew.

THE TEETH OF CARNIVORA.

THE animals grouped together under the name of Carnivora are divided into two sections, the Aquatic and the Terrestrial Carnivora.

The terrestrial Carnivora were formerly classed as "digitigrade" and "plantigrade," a classification exceedingly inconvenient, as it left the greater number of the animals to be classified in the debateable ground between the two extreme types. As a linear classification is impossible, they are now grouped around three centres: the Œluroidea, or cat-like; the Cynoidea, or dog-like; and the Arctoidea, or bear-like Carnivora; and, instead of taking the Felidæ, or Cats, as the type of the group, it is generally considered that the Dog tribe are the most generalised form, and that the Cats are an extreme modification in one direction, the Bears in another.

The Cynoidea comprise the Dog, and its immediate allies, the Wolves and Foxes.
The Œluroidea, or Cat-like Carnivora, comprise the Viverridæ (Civets), Hyænas, and Cats.
The Arctoidea, or Bear-like Carnivora, comprise the Mustelidæ (Weasels), Procyonidæ (Racoons), and the true Bears.

The order Carnivora is a very natural one, and its name is, upon the whole, fairly descriptive of the habits of the majority of its members; though there are some creatures included in it which are mixed feeders, and others which are purely vegetarian.

In carnivorous animals one tooth on each side of both upper and lower jaws is of considerable length, is sharply pointed, and is called a canine; the upper canine is separated by an interval from the incisors, the lower canine

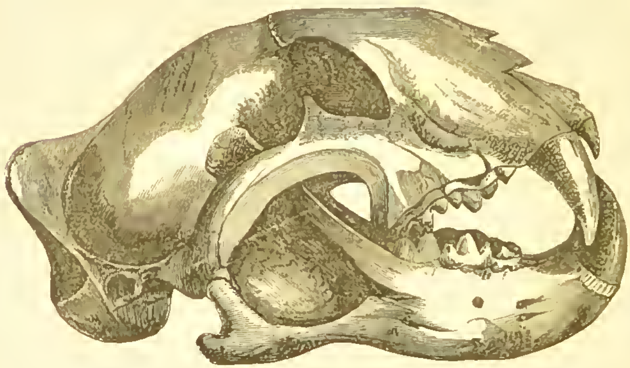
being received into the vacant space or "diastema" so formed.

The incisors are short, almost always six in number, and stand nearly in a straight line, transversely across the front of the jaw, the outermost upper incisor being sometimes large and pointed so as to be like a small canine.

The incisors and canines may, on the whole, be said to be tolerably uniform throughout the order, but the variations in the premolar and molar teeth are both numerous and interesting.

In the most purely carnivorous members of the order,

FIG. 181 (1).



the Felidæ, the true molars are reduced to a minimum, and the back teeth are thin edged, "sectorial" teeth; in the bears, on the other hand, some of which are purely herbivorous, the molars are little short of the full typical mammalian number, and are furnished with obtuse and broad grinding surfaces.

The accompanying figure will serve to give the general aspect of the teeth and jaws of a typically carnivorous animal, and to show the great development of the processes

(1) Side view of the cranium of a Tiger, with the mouth slightly opened to show the relative position of the great canines.

for the attachment of muscles, and the stout wide arch of the zygoma.

To a particular tooth in the upper jaw, and to its antagonist in the lower jaw, Cuvier gave the name of "carnassial;" these, conspicuous in the true flesh-feeders, become less differentiated in the Arctoidea or bear-like Carnivora, and in the bears themselves are indistinguishable from the other teeth, save by a determination of their homologies by a process of comparison with the teeth of intermediate forms.

The sectorial or carnassial tooth in the upper jaw is always the fourth premolar; its crown is divisible into two parts, the one a thin sharp-edged blade, which runs in an antero-posterior direction, and is more or less divided by one or two notches into a corresponding number of cusps; the other part, the "tubercle," is a shorter and blunter cusp, and supported upon a distinct inner root situated at the inner side of the anterior end of the blade (see fig. 182). In those which are most purely flesh-feeders, the "blade" is well developed, and the tubercle of small size; an increase in the tubercular character of the tooth is traceable through those genera which are mixed feeders.

Thus in the bears the tubercle is said to be highly developed, but it is to be noted that the large flattened inner portion of the bear's sectorial tooth is in a more posterior position than the tubercle of a cat's sectorial, and is not supported upon any separate root.

The lower tooth which antagonises the upper carnassial, passing a little behind it, is the first true molar; in the Felidæ it consists solely of the blade, which is divided into two large cusps, behind which is a very small and rudimentary third division (which in the Hyænidæ, for example, is of conspicuous dimensions). In existing Carnivora but one "sectorial" tooth is to be found on each side of the jaws, but in the Hyænodon, which had the full number of 44 teeth,

and in some other extinct tertiary mammals there were more teeth partaking of this character.

In a general sense we may say that the characters which indicate a pure flesh diet are: the small size of the incisors as compared with the canines, and their arrangement in a straight line across the jaw; the large size, deep implantation, and wide separation from one another of the canines; the reduction in number of the molar series, those that remain being without broad crushing surfaces, in the place of which a pointed or sharp-edged form prevails.

Thus the more numerous the teeth of the molar series, and the broader their crowns, the more likely it is that the creature subsists upon a mixed diet; and a gradation may be traced even in individual teeth, such as the carnassials, in which a gradual increase in relative size of the internal tubercular cusps of the upper, and of the posterior tubercles of the lower teeth, may be traced as we pass from the examination of the teeth of Felidæ, to those of mixed feeders, such as the Arctoidea.

It is a familiar observation that immature animals differ less from their allies than do the respective adults, and this is exemplified by the milk dentition of the present order.

With the exception of the Felidæ, which have only two lower milk molars, the terrestrial Carnivora, so far as is known, all have the same milk dentition:

$$\mathrm{i}\,\frac{3}{3}\;\mathrm{c}\,\frac{1}{1}\;\mathrm{m}\,\frac{3}{3}.$$

Cynoidea.—The dog presents almost the full typical number of teeth, one upper molar (present in an extinct dog-like animal, the Amphicyon) alone being wanting.

$$\mathrm{i}\,\frac{3}{3}\;\mathrm{c}\,\frac{1}{1}\;\mathrm{pm}\,\frac{4}{4}\;\mathrm{m}\,\frac{2}{3}.$$

The incisors are small, the outermost being the largest; the upper incisors have, as in a great many Carnivora, a

tri-lobed shape, the surface of the crown being marked by a transverse groove into which the apex of the lower tooth fits, and the anterior of the lobes thus formed being notched so as to divide it into two.

FIG. 182 (1).

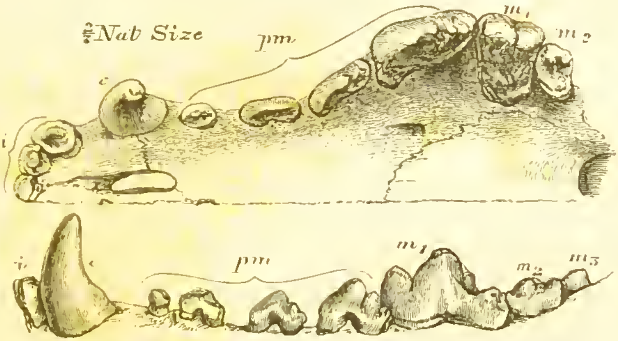


FIG. 183 (2).

The canines, large and conical, are somewhat compressed from side to side, and have an anterior and a posterior sharp ridge; they are also slightly flattened on their inner surface. The premolars are flattened from side to side, pointed, increasing in size from before backwards, and have small

(1) Dentition of Australian Dog (Canis Dingo).
(2) Milk and permanent teeth of Dog (after Prof. Flower).

basal accessory cusps (see fig. 182). The fourth upper premolar is the sectorial tooth, and is very much larger than the third premolar; the blade is well pronounced, and the tubercle small. The fourth lower premolar does not greatly differ from the third. The two upper true molars are blunt, broad-crowned tuberculated teeth, but the second is very small.

In the lower jaw the first true molar or carnassial tooth has a well-marked blade, which articulates with the blade of the upper carnassial tooth; but towards the posterior border there is a somewhat thick and blunt tuberculate portion, barely represented in the corresponding tooth of the Felidæ; the tubercular portion articulates with the broad flat first upper molar. The second lower molar is smaller, not being one-fourth the size of the first; the third smaller still; both are blunt-crowned tuberculated teeth (the third lower molar, rudimentary in all dogs, is altogether absent in the Canis primævus). The fox-like Otocyon, however, has m $\frac{4}{4}$, making up a total of 48 teeth, an excess over the full mammalian dentition.

The dentition of the dog, closely similar as it is to that of the wolves and foxes, is such as to allow of a considerable range of diet, there being tubercular molar teeth in addition to a full armament of such sharply-pointed teeth as are characteristic of flesh-feeding animals.

Thus the Canidæ, uniform as they are in dentition, have somewhat different habits; the Arctic fox, a flesh-feeder purely, has a dentition indistinguishable from the North Italian fox, which is reputed to be vegetarian in its diet; the Canis cancrivorus of Guiana, which often possesses a fourth molar, eats small mammals, crabs, and also fruit. Hence it is necessary to be very careful in deducing from the character of the teeth what may probably have been the diet of the animal; an approximate idea may often be

reached, but the sources of fallacy are sufficiently numerous to render the conclusion uncertain.

Amongst the various breeds of dogs some slight differences exist. Thus in the long-muzzled races considerable intervals exist between the premolars, as is to some extent seen in C. Dingo (fig. 182), while in the short-muzzled races the teeth are in contact, and set somewhat obliquely, so as to be almost imbricated.

On the whole it may be said that the teeth are less easily susceptible of modification in size than are the jaws, so that crowding of the teeth is induced by selective breeding aiming at the production of short-muzzled varieties.

In some long-muzzled races supernumerary teeth are sometimes found; thus De Blainville (Ostéographie, *Canidæ*) figures two examples, the supernumerary tooth being in one case a premolar, in the other a true molar.

Œluroidea.—With a dental formula not differing much from the dog (and not at all from Canis primævus) the Viverridæ (Civet cats, Ichneumons, &c.), approach the more typical carnivores in such points as the thinner and sharper blades of the premolar teeth and the greater relative length and sharpness of the canines.

The dental formula is

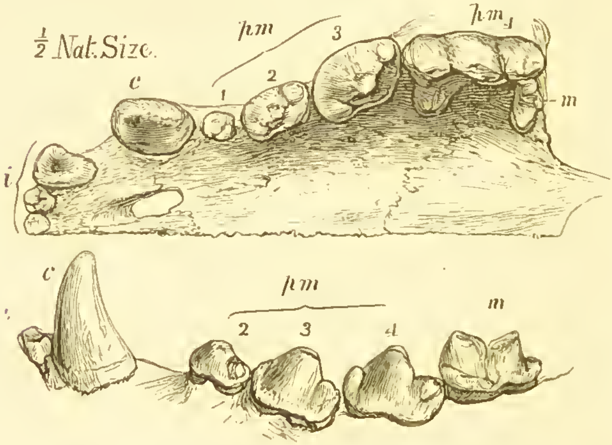
$$i\,\frac{3}{3}\;c\,\frac{1}{1}\;p\,\frac{4}{4}\;m\,\frac{2}{2}.$$

At the same time the lower carnassial tooth has no less than six sharply pointed cusps, and it lacks the typical character of a sectorial tooth, while the long pointed cusps of the molars of some Viverridæ recall the characters of insectivorous dentitions rather than those of true flesh-feeders; furthermore, there are other Viverridæ which are not at all savage, and which subsist on a diet of fruits, eggs, &c., such as the Binturong or the Paradoxurus, the

teeth of which have almost lost the carnivorous character. Little use can therefore be made of the Viverridæ as illustrating the transition between the dental characters of the other families of the order; they rather serve to exemplify how, within the limits of a single family, with an identical dental formula, the form and size of the teeth may vary so as to adapt its members to different forms of food and habits of life.

Hyænidæ.—In the Hyæna the jaw is short and stout; the

FIG. 184 (1).



canines are set far apart, and the teeth of the molar series are reduced in number.

$$i\ \frac{3}{3}\ c\ \frac{1}{1}\ p\ \frac{4}{4}\ m\ \frac{1}{1}.$$

The incisors are short and stout, but the outermost upper incisor is somewhat caniniform; the canines are very

(1) Upper and lower teeth of Hyæna. The strongly marked cingulum is seen upon the lower teeth. In the upper jaw the fourth premolar (carnassial tooth) has a strong blade, divided into three cusps, and a small tubercle opposite to and within the anterior cusp; it is a good typical carnassial tooth.

strong, but are not so long relatively to the other teeth as in the Felidæ.

The premolars are all stout pointed teeth, with a very well pronounced basal ridge or cingulum, serviceable in protecting the gums when the creature is crushing up bones; they increase in size from before backwards in the upper jaw, the fourth upper premolar being a well-marked carnassial tooth with its blade and tubercle.

The lower carnassial or first molar consists of little more than the notched blade; but the little posterior tubercle so strongly pronounced in the dog, is in the hyæna distinctly more marked than in the Felidæ (cf. figs. 184 and 185). The only upper true molar is the rudimentary tooth, placed inside the back of the fourth premolar.

The main feature of the dentition of the hyæna is the great stoutness and strength of the teeth; they are admirably adapted to the habits of the animal, which feeds rather upon the portions of Carcasses left by the fiercer carnivora than upon those which it kills for itself, and consequently bones form a large proportion of its food.

There is a curious hyæna-like animal found at the Cape (of which there are often specimens at the Zoological Gardens) called Proteles or Aardwolf, in which the teeth of the molar series are quite rudimentary. The incisors (much worn in old animals) and the canines are fairly well developed; the molars and premolars quite stunted.

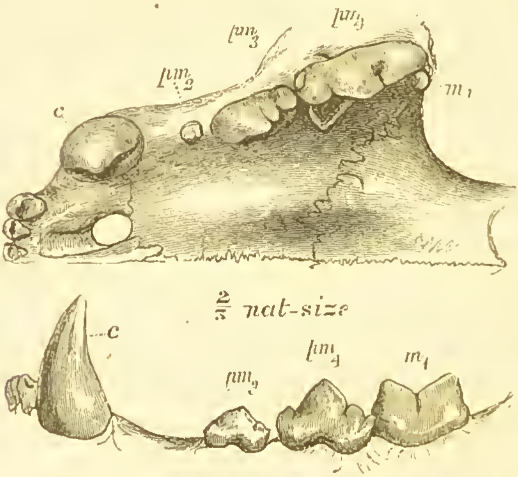
The deciduous dentition $\left(\text{dm. } \frac{3}{3}\right)$ is similar to the adult, as respects the teeth being stunted. It is a cowardly animal, and is supposed to feed on putrid flesh; it is said to eat young lambs, and to bite the large tails of the Cape sheep, which are remarkable for containing an abundance of semi-fluid fat.

Felidæ.—The dentition of this family is singularly uniform.

$$i\ \frac{3}{3}\ c\ \frac{1}{1}\ p\ \frac{3}{2}\ m\ \frac{1}{1}.$$

Thus the molar series is reduced below that of hyæna by the loss of a premolar in both jaws. The incisors are very short, the canines very large, widely apart, and sharply pointed, with a pronounced longitudinal ridge very characteristic of the Felidæ; the premolars nearest to them are

FIG. 185 (1).



quite short, so that they stand practically alone, and so can penetrate the flesh of living prey more readily.

The first upper (really the second of the typical mammalian dentition) premolar is almost a rudimentary tooth; the second, a far larger tooth, is sharply pointed; the third is a well pronounced carnassial tooth, of which the "blade" is divided by two notches into three sharp lobes, with the middle one of which the "tubercle" is connected by a slight ridge.

The solitary true molar is a small tooth, placed trans-

(1) Side view of lower, and palatal aspect of upper jaw (Leopard).

versely, and within the back of the premolar, so that looking from the outside it is not visible at all.

In the lower jaw the carnassial (first molar) is reduced to the "blade" only; it is divided by a V-shaped notch into two lobes, and the posterior tubercle is hardly represented.

In an extinct feline animal, the Machairodus, found in tertiary strata, and very widely distributed (in France, Italy, India, Brazil, Buenos Ayres) the first of the premolars left in the upper jaw of Felis, and there almost rudimentary (see fig. 185), has disappeared; the dental formula is thus:

$$i\ \frac{3}{3}\ c\ \frac{1}{1}\ p\ \frac{2}{2}\ m\ \frac{1}{1}.$$

The upper canines are of immense length, and the ridge of enamel which runs down the front and back surface of

Fig. 186 ([1]).

the teeth is distinctly serrated; hence the name of saw-toothed Tiger which has been given to the animal.

The lower canines are quite small, and ranged with the

([1]) Side view of the jaws and cranium of Machairodus (Drepanodon), after Owen.

incisors. The enormous length of the upper canine renders it difficult to see in what manner it was made use of, as the mouth could hardly have been opened to an extent sufficient to enable its point to do more than clear the lower jaw.

Smilodon, a somewhat similar extinct animal, had a dentition still further reduced, viz. :

$$i\ \frac{3}{2}\ c\ \frac{1}{1}\ p\ \frac{2}{2\text{ or }1}\ m\ \frac{0}{1}.$$

Prof. Cope has described a rich series of extinct cats ("Extinct Cats of N. America," American Naturalist, Dec. 1880), mostly from Miocene beds. He summarises their characters thus :

"It is readily perceived that the genera above enumerated form an unusually simple series, representing stages in the following modification of parts :—

(1.) In the reduced number of molar teeth.
(2.) In the enlarged size of the upper canine teeth.
(3.) In the diminished size of inferior canine teeth.
(4.) In the conic form of the incisors.
(5.) In the addition of a cutting lobe to the anterior base of the upper sectorial tooth.
(6.) In the obliteration of the inner tubercle of the lower sectorial.
(7.) In the extinction of the heel of the same.
(8.) In the development of an inferior flange at the latero-anterior angle of the front of the ramus of the lower jaw.
(9.) In the development of cutting lobes upon the posterior border of the large premolar teeth.

The succession of the genera above pointed out, coincides with the order of geologic time very nearly.

The relations of these genera are very close, as they differ in many cases by the addition or subtraction of a single tooth from each dental series.

These characters are not even always constant in the same species, so that the evidence of descent, so far as the genera are concerned, is conclusive. No fuller genealogical series exists than that which I have discovered amongst the extinct cats."

The extinct Hyænodon in some respects resembled the Felidæ, though it is on the whole of somewhat doubtful affinities: it differed in that it presented the typical mammalian formula of

$$i\,\frac{3}{3}\;c\,\frac{1}{1}\;p\,\frac{4}{4}\;m\,\frac{3}{3},$$

its great peculiarity being that one and all of these teeth were of "carnassial" (1) form. Yet the elongated form of its jaw is, so far as it goes, opposed to the idea of its having been highly carnivorous; its food at all events must probably have consisted of animals very much smaller than itself.

Arctoidea.—Amongst the Carnivora grouped together by many characteristics as 'bear-like,' a tolerably complete gradation of character in the matter of dentition may be traced.

Some of the group, such as the stoats and martins, are very carnivorous; others are mainly herbivorous. Of the Mustelidæ the dental formula is

$$i\,\frac{3}{3}\;c\,\frac{1}{1}\;p\,\frac{4}{4}\;m\,\frac{1}{2}.$$

There is a sort of *primâ facie* resemblance to the feline dentition, for the sectorials are very much like those of the Felidæ, but the last tooth in each jaw is a broad topped tubercular molar, even in the most carnivorous members of the group, while in those which are less so, such as the badger, the molar teeth are very broad and obtuse, the

(1) The carnassial tooth of Felidæ is always opposite to the corner of the lips: if further forward it would act at a disadvantageous leverage, and if further back, could not be got at for slicing pieces off a carcase too large to take bodily into the mouth (Cope.)

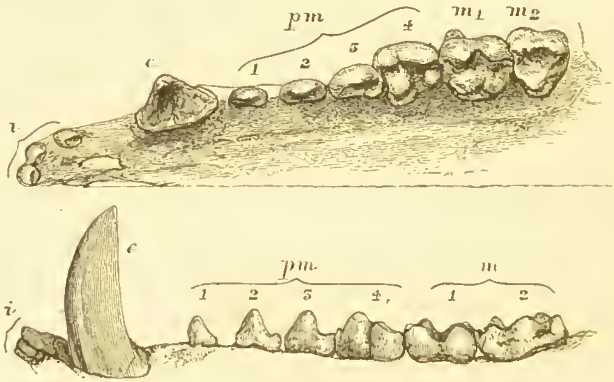
lower sectorial having a very small blade and a very large tubercular posterior talon, so that, without having really lost its typical formation it comes practically to be a broad grinding tooth.

In the Procyonidæ (Racoons and Coatimundis, &c.), we have a further departure from the carnivorous character, in the increased development of the molar series: the dental formula is

$$i\,\frac{3}{3}\;c\,\frac{1}{1}\;p\,\frac{4}{4}\;m\,\frac{2}{2}.$$

In the Coatimundi, for example, the upper sectorial

Fig. 187 (1).



has a very large "tubercle," and posteriorly to this there is a small additional tubercle; the "blade" has no large or conspicuous thin, flat, sharp edge, but presents two pronounced cusps.

The lower sectorial is no longer recognisable as a carnassial tooth, and all the true molars are broad teeth with four or five cusps.

(1) Upper and lower teeth of a Coatimundi (Nasua socialis). The fourth upper premolar (carnassial tooth) has lost its sectorial character by the blade being much less, and the tubercle much more, developed than in the Æluroidea; there is an additional internal tubercle at the back of the tooth.

The canines are very peculiar, those of the upper jaw being very straight and much flattened from side to side; those of the lower jaw strongly curved, and marked by a deep groove near the front of their anterior surface.

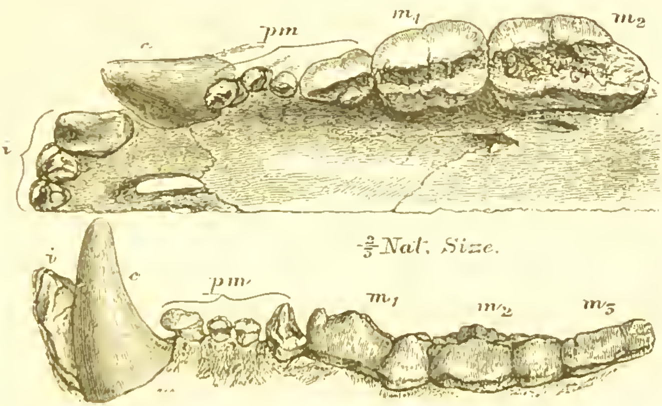
In the Bears the teeth are yet further modified to suit the requirements of mixed or vegetable feeders.

The dental formula is generally—

$$i\ \frac{3}{3}\ c\ \frac{1}{1}\ p\ \frac{4}{4}\ m\ \frac{2}{3}.$$

The incisors of the upper jaw present the notch across the crown, so common in Carnivora, and the outermost is

FIG. 188 (1).



large and not unlike a canine; the canines are, relatively to the other teeth, not so large as in dogs or Felidæ; nevertheless they are stout strong teeth, upon which the anterior and posterior ridges of enamel are well marked.

The first three premolars are small dwarfed teeth; the first premolar is very close to the canine, and has a crown of peculiar form, produced out towards the canine.

(1) Teeth of a Bear (Ursus thibetanus?). The figure is drawn from a young specimen, in which the canines have hardly attained to their full length. In this bear the four premolars are all persistent.

All four of the premolars seldom persist through the lifetime of the animal; the first premolar, however, is rarely (if ever in recent species) lost, the second being the first to fall out, and then the third. As the fourth is never lost, in most adult bears the first and fourth premolars are found, with a wide interval between them. The premolars of bears thus form an exception to the rule that when a tooth is lost from the premolars, the loss takes place from the front of the series.

The fourth upper premolar (carnassial tooth) retains something of its carnassial character, though relatively to other teeth it is smaller than in the Felidæ; the first lower molar very little, save that it is a narrower and more elongated tooth than the other true molars.

The other true molars are squarish or oblong teeth, raised into blunt tubercular cusps; they vary in different species.

In the sloth bear (Melursus labiatus) the incisors are small and the median pair are lost early; it is variously stated to be frugivorous and to feed on ants, the latter probably being the more truthful account.

Carnivora Pinnipedia (Seals).

The aquatic Carnivora are divided into three families:—

I. The Otariidæ, or Eared Seals, comprising the single genus Otaria, known as Sea Lions, or Sea Bears. These are the "fur Seals," from which seal skin is procured, and they are less removed from the terrestrial carnivora than are the other seals: the limbs are better adapted for walking, there are external ears, &c.

II. The Phocidæ, to which family the seals of our own coasts (Phoca greenlandica, &c.) and the Great Proboscis Seals of the southern seas (Cystophora) belong.

III. The Trichechidæ, or Walruses, an aberrant Arctic family consisting of one genus only.

The dentition of the seals is less highly specialised than

that of other Carnivora, in some cases approximating to that of homodont Cetaceans.

The seals belong to the less powerfully developed orders of

Fig. 189 [1].

mammalia, and like others similar in this respect, have no change of functional teeth.

What change there is takes place at an exceedingly early period, indeed at or before birth.

[1] Jaws of Otaria, in which the teeth are affected by a form of erosion. After Dr. Murie. Odont. Soc. Trans., 1870.

The milk dentition is very feebly developed in all seals; in the Otaria (fur seal) which of all the seals most approaches to the terrestrial carnivora in other characters, the milk teeth are retained for a few weeks, but in most others they are shed about the time of birth. Thus Professor Flower tells us that in a Phoca greenlandica a week old scarcely a trace of the milk teeth was left.

The canines are generally well marked by being larger than the other teeth, but the molars and premolars are very similar to each other, and are simple in pattern.

The teeth of Otaria and of some other seals become

FIG. 190 (1).

much worn down, and they also seem to become eroded at the level of the gums, as they are often deeply excavated at points which seem unlikely to have been exposed to friction, but the nature of this erosion has not been adequately investigated.

The incisors, however, vary in number in different groups, while the canines, premolars, and molars are constant.

The common seals (Phoca) have a dental formula

$$i\ \frac{3}{3}\ c\ \frac{1}{1}\ p\ \frac{4}{4}\ m\ \frac{1}{1}.$$

The incisors are of simple form, and the outer are the larger. The canine is a strong recurved tooth, with a large root; behind it follows a series of molars, each of

(1) Teeth of Phoca greenlandica.

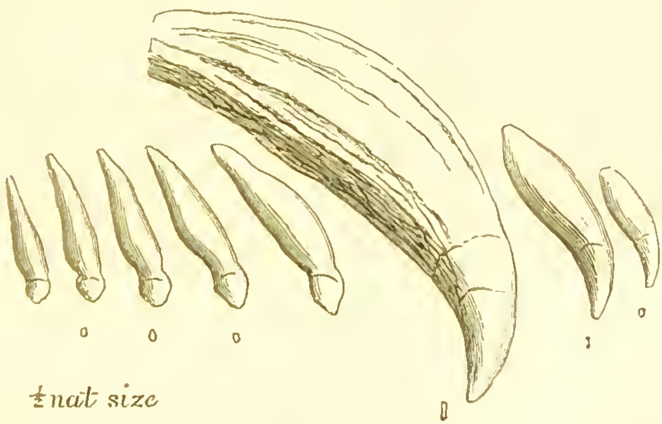
which (with the exception of the first) bears a central principal cusp, with a smaller accessory cusp before and behind it. The forms of the crowns vary a good deal in different genera, in some the cusps being much larger, more deeply separated from one another and recurved; and in others the accessory cusps being multiplied, so that the name of "saw-toothed seal" has been given to their possessor.

It is suggested by Baume that the degree to which the teeth have become simplified perhaps corresponds with the antiquity of the genus as aquatic, those which have taken to the water more recently having retained a greater complexity of tooth crown.

The Leopard Seal has teeth with exceedingly long roots, disproportionate, one would say, to its necessities for firm implantation of its teeth.

In the Hooded seals (Cystophora) the incisors are reduced

FIG. 191 ([1]).

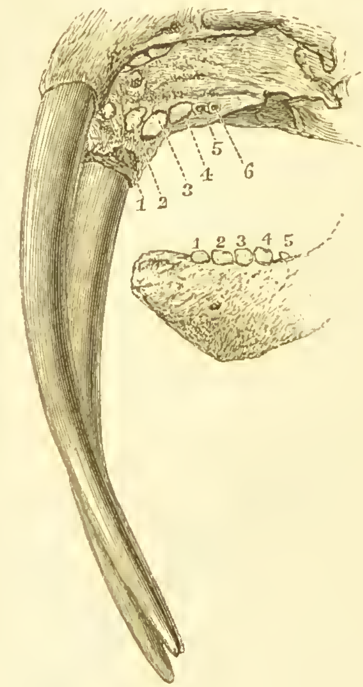


to one in the lower jaw and two in the upper; the canines are of great size, but the molars are small and simple in form, so as to approximate to the teeth of the Cetacea.

([1]) Permanent and milk teeth of Elephant Seal (Cystophora proboscidea).

The walrus (Trichechus rosmarus), an aberrant Arctic form, is possessed of enormous upper canines, which pass down outside the lower lip, and are of such dimensions as to materially modify the form of cranium by the size of their sockets ; they grow from persistent pulps, and are composed of dentine with a thin investment of cement.

Fig. 192 (1).



The great tusks are employed to tear up marine plants and to turn over obstacles, the walrus feeding upon crustacea, and also upon seaweed, &c. ; they are also used to

(1) Side view of upper and lower jaws of a Walrus (Trichechus rosmarus). The upper jaw has been tilted a little to one side, in order to bring into view the molar teeth at the same time with the long tusks. The determination of the teeth being open to question, they have been simply numbered.

assist the animal in clambering over ice: as they are of almost equal size in the female, they cannot be regarded as weapons of sexual offence, but they are undoubtedly used in the combats of the males.

The largest tusks seen by Nordenskiold were 30 inches in length, and 8 inches in circumference; the tusks of the females attain to the same length, but they are much more slender.

In addition to the great tusks the walrus ordinarily has a row of four or five teeth, short and simple and worn down to the level of the gums. Of these, the one placed immediately within the base of the great canine is in the intermaxillary bone, and is hence an incisor: the ordinary dental formula is given by Professor Flower as

$$i\,\frac{1}{0}\;c\,\frac{1}{1}\;p\,\frac{3}{3}.$$

But there is some difficulty in assigning a definite dental formula: for in front of the solitary incisor are often the sockets (or even the teeth themselves) of two others, which are for various reasons rather to be regarded as non-persistent teeth of the permanent set than as milk teeth; and there are also small teeth sometimes to be met with behind the molars, which seem to be rudimentary permanent teeth.

In young specimens the dentition is

$$i\,\frac{3}{3}\;c\,\frac{1}{1}\;\text{pm and m}\;\frac{5}{4}.$$

The teeth above alluded to may persist through life, and probably often do; but they are sure to be lost in macerated skulls, as they have but little socket. Of the milk dentition four teeth have been traced in each jaw; they are rudimentary, are lost about the time of birth, and correspond in position to the more largely developed teeth of the

adult. Hence the question if those small rudimentary teeth above alluded to are to be regarded also as milk teeth which are long retained, or as rudimentary permanent teeth; at present this requires further elucidation.

The Teeth of Primates.

The order Primates embraces Man, Monkeys, and the Lemurs.

Some naturalists have been disposed to separate the Lemuridæ from the rest of the Primates, on the ground that some Lemurs approximate rather closely to the Insectivora, while again the order Insectivora contains some forms which recall the Lemurs.

Prof. Cope regards the Lemurs as an exceedingly ancient and generalised form, and considers that they may have been parent forms of many widely different mammalian forms.

But although the Lemuridæ are undoubtedly inferior to the Monkeys, and stand apart from them more widely than do the Monkeys from Man, most authors now place them in the order Primates, which is to be divided as follows:—

Primates	Lemuridæ.	Lemurs.
	Simiadæ	Old and new world Monkeys.
	Anthropidæ.	Man.

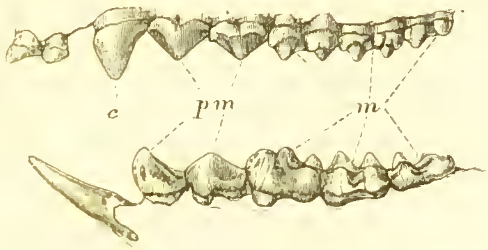
Lemuridæ.—The Lemurs for the most part are found in Madagascar, and to a less extent on the mainland of Africa and in southern Asia. In their dentition, just as in other characters, they differ somewhat from the true monkeys, though, on account of there being several very aberrant in form, it is difficult to give any general account of them. Most of them have the upper incisors very small, and widely separated from one another; in the lower jaw these are antagonised by six or eight long, thin, narrow procumbent teeth, generally regarded as being two pairs of incisors and the lower canines: in both upper and lower jaws the next tooth is

large and pointed like a canine, but the lower caniniform tooth bites behind the upper, and so is held not to correspond to it, but to be the first premolar. The premolars are compressed from side to side, and are very sharp : the molars are armed with long sharp cusps, which are worn down in old animals.

The upper molars in many lemurs are armed with four cusps, connected by an "oblique ridge" like those of man and the anthropoid apes.

In many of them the lower premolars are two rooted, the roots being more or less completely in the position of outer and inner, not of anterior and posterior roots.

FIG. 193 (1).



There is a very aberrant lemur, the Aye-aye (Cheiromys), which in its dentition imitates the rodents.

$$i\ \frac{1}{1}\ c\ \frac{0}{0}\ pm\ \frac{1}{0}\ m\ \frac{3}{3}.$$

In both upper and lower jaws the incisors form a single pair of large curved teeth, growing from persistent pulps, and wearing obliquely so as to constantly preserve a sharp cutting edge. The enamel is very much less thick, if not altogether absent, upon the backs of the upper incisors, but

(1) Teeth of the Indri.

the lower incisor, which is very narrow from side to side, and very thick from baek to front, is composed very largely of enamel, the dentine eonstituting but a very small part of it.

After a eonsiderable interval, which is devoid of teeth, there follow four upper and three lower teeth, which are not of persistent growth, but have definite roots, and resemble the molars of many omnivorous rodents.

Being a somewhat rare and strietly noeturnal animal, little is known of its food; some have believed that it makes use of its rodent ineisors to cut away portions of wood in order to get at the grubs contained in it, drawing them out of their hiding place by means of its curiously elongated finger, whilst others believe that it gnaws the sugar cane. But whatever the nature of its food may be, it is certain that its scalpriform incisors are put to hard work, and so kept worn down, for in a specimen kept for a time in the Zoological Gardens, whieh was supplied with soft food, the ineisor teeth grew to an excessive length, and ultimately caused the animal's death by the points of its lower incisors perforating the palate. The aecompanying figure represents the muzzle of this speeimen, and although the upper teeth have grown to an inordinate length, and have diverged from one another, it will serve to show the rodent-like aspeet of its mouth.

Although, functionally, its teeth are those of a rodent, yet despite this adaptive resemblanee, the milk dentition retains certain characters which indicate the lemurine origin of the creature.

In the upper jaw the milk dentition consists of two small incisors, a canine and three molars; in the lower jaw of two small incisors and two small molars; it is said that in an early stage a third milk ineisor is to be found.

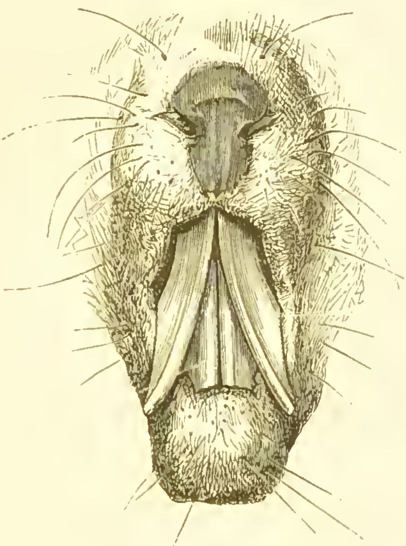
The permanent incisors push their way up between the first and second milk incisors; at a eertain stage all three

are to be seen at once, but the large size of the permanent incisors causes the speedy loss of the milk incisors.

No known rodent has so many milk teeth, nor indeed any milk incisors at all ; the Aye-aye thus affords an excellent example of a milk dentition preserving characters which are lost in the extremely modified adult dentition.

The special interest which attaches to the dentition of

Fig. 194 (1).

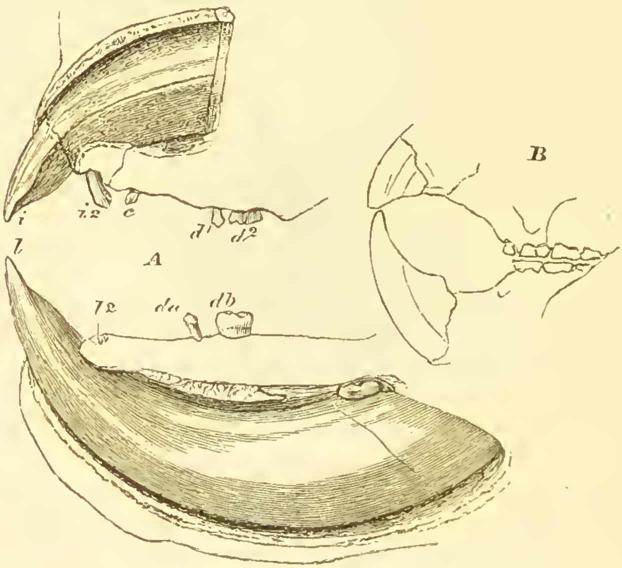


Cheiromys has been already alluded to ; to briefly recapitulate, it is this : in Madagascar, an isolated area separated by a wide tract of deep sea from other areas, true rodents are almost absent, but lemurs abundant. But one of the lemurine animals which are to be found there has been so modified that its teeth to all intents and purposes

(1) Aye-Aye (Cheiromys), which died in the Zoological Gardens (after Dr. Murie). The upper incisors, from want of sufficient use, have grown long and diverged from the middle line.

are those of a rodent. Yet with all this modification it retains characters (notably its milk dentition) which are quite unlike those of true rodents, but which recall the manner of its origin from higher lemurine forms.

FIG. 195 [1].



Simiadæ. — The true monkeys are divided into two great divisions, the new world monkeys and the old world monkeys. The former differ in many respects from the latter; for the most part they have prehensive tails, and their nostrils are set somewhat widely apart, whence they are called *Platyrrhine*, or wide-nosed monkeys, and they differ also in their dental formula, which is—

[1] Upper and lower jaws of Cheiromys. A. Milk dentition, with the permanent incisors just emerging. *i*, *l*. Upper and lower permanent incisors. *i* 2, *l* 2. Upper and lower milk incisors. *c*. Milk canines. *d* 1, *d* 2, *d a*, *d b*. Upper and lower milk molars. (Twice natural size.) B. Reduced figure of permanent teeth (after Peters).

$$i\,\frac{2}{2}\,c\,\frac{1}{1}\,p\,\frac{3}{3}\,m\,\frac{3}{3}=36.$$

The little marmoset monkeys have only 32 teeth, but they agree with the other new world monkeys in having three premolars on each side, the molars being reduced to two in number. The upper molars of some new world monkeys, notably Ateles and Mycetes, have the antero-internal and extero-posterior cusps joined by an oblique ridge, a character which is shared in the old world groups by man and the anthropoid apes only.

In the spider monkeys (Ateles) the outer lower incisors are caniniform, and the canines which are long and sharp are very like the anterior premolars, but have their outer cusps much longer. The inner cusp of the anterior lower premolar is hardly developed, but in pm_3 the inner cusp and posterior cingulum is more pronounced, and in pm_4 it is yet more strongly expressed: they are all single rooted, and show the relationship of the canine to the premolars excellently well.

The upper premolars, especially the last, have roots bifurcated near their tips, but have not three roots. The bifurcation in the root of m_1 takes place only low down, in m_2 lower still, and m_3 is single rooted and small, so that the teeth show a tendency to reduction.

Of the upper molars the first two are three rooted, but the third is hardly even bifurcated.

All Quadrumana have well developed milk dentitions.

Old world or *Catarrhine* monkeys all have the same dental formula as man—

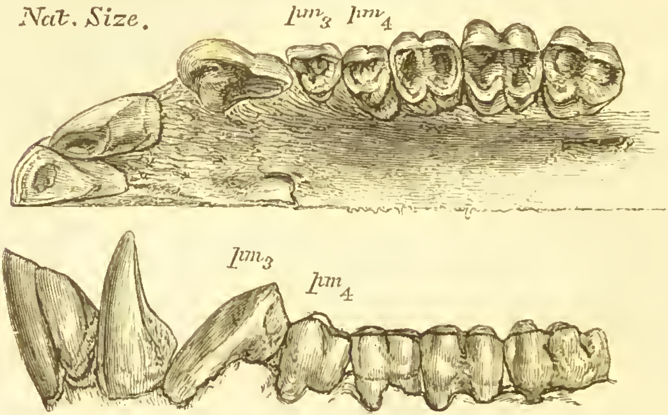
$$i\,\frac{2}{2}\,c\,\frac{1}{1}\,p\,\frac{2}{2}\,m\,\frac{3}{3}.$$

As an example the Macaque monkey may be taken. The upper and lower incisors, but especially the former, are directed obliquely forwards, and the lateral incisors are very

much smaller than the centrals. In the upper jaw a considerable interval separates the incisors from the canine, which is a very large tooth, somewhat triangular in section, with a sharp edge directed backwards, and with a deep groove on its anterior surface.

The upper premolars are implanted by three distinct

FIG. 196 (1).



roots, as are also the true molars; the latter are quadricuspid, but lack the oblique ridge.

The lower canine is a sharp and powerful tooth, though it is very much smaller than the upper; the first lower premolar, by its front surface, articulates with the upper canine, and is of curious form. It is implanted by two roots, but the anterior root is produced forwards, so that the antero-posterior extent of the tooth is much increased.

The apex of the cusp of the tooth is almost over the posterior root, and from this point the crown of the tooth

(1) Upper and lower teeth of a Monkey (Macacus nemestrinus, male). The length and sharpness of the canines, and the peculiar form of the anterior lower premolar, contrast with the aspect of the corresponding teeth in the Anthropoid Apes or in Man.

slopes obliquely forwards down to its anterior root. This peculiarity in the form of the first lower premolar is eminently characteristic of the baboons. There is nothing to note of the second premolar save that it is implanted by two roots, like the true molars, which are quadricuspid; of them the third is larger than the first two, and is quinquicuspid.

But in some genera, *e.g.* Cercopithecus, this is reduced in size and is tricuspid.

There is considerable difference in the size of the canine in the two sexes, that of the male being very much the larger; this difference does not exist in the deciduous dentition, in which the canines are relatively small.

The Anthropoid Apes are the Gibbons (Hylobates), the Chimpanzee (Simia troglodytes, or Troglodytes niger), the Orang (Simia or Pithecus satyrus), and the Gorilla (Troglodytes gorilla).

Upon the whole the gibbons are the lowest, and the gorilla the highest of the anthropoid apes, which are all confined to tropical areas. Thus the gorilla and chimpanzee are confined to tropical Africa, and the orang is limited to a part of the Malay archipelago. The gibbons are more widely distributed over the Malay archipelago and tropical Asia.

Although upon the whole the gorilla approaches most nearly to man, this can hardly be said to be the case with its dentition. The jaws are very square, and there is a large diastema in front of the upper canine, which in the male gorilla is of great size and strength, its top descending far below the level of the alveolar border of the lower jaw when the mouth is shut.

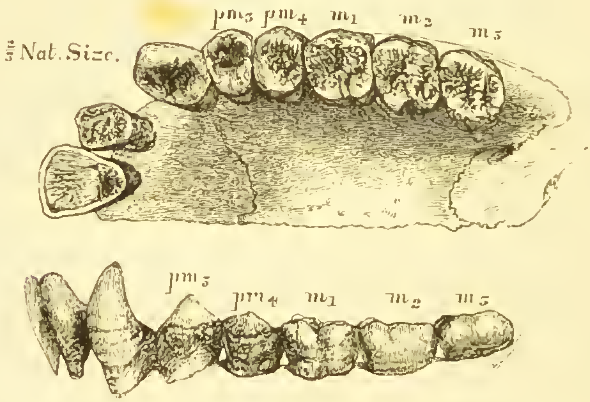
In the lower jaw there is no diastema, but the teeth are all in contact with one another; the first of the premolars is a very strong pointed cone, showing plainly the close relationship between canines and premolars alluded to at a previous page.

The molars increase in size from before backwards, the third molars attaining to a very large size.

Nevertheless, though the teeth are coarser and stronger, there is a general resemblance to those of man.

It has been pointed out by the late Professor Rolleston that the canine tooth of the male anthropoid apes is a little later in coming into place than in the female. Thus in the male chimpanzee and orang, it is not cut until after the third

FIG. 197 ([1]).



molars (wisdom teeth) are in place, whereas in the female it follows the second, but precedes the third molars. The sexual difference in the canine teeth is very well marked in all the anthropoid apes, and its later eruption in the males is explicable both upon the ground that, being a sexual weapon, it is not needed prior to the attainment of sexual maturity, and also that being of very large size its formation might be expected to take a longer time. No such difference pertains to the milk dentition, in which the order of eruption is exactly that met with in man.

Dr. Magitot (Bulletin de la Société d'Anthropologie de Paris, 1869) combats the idea that there is any difference in

([1]) Upper and lower teeth of an Anthropoid Ape (Simia satyrus, or Orang Outan).

the order of the eruption of the permanent teeth between man and the anthropoid apes, but, while his observations have been both careful and widely extended, he lays much stress upon an observation made upon a *female* gorilla skull, in which, as has just been mentioned, the order of succession is not quite the same as in the male.

In a specimen of a New World Monkey (Cebus hypoleucus) I have found m_3 on the point of erupting, whilst the temporary milk molars had not yet been shed, and its canine was not yet erupted.

Prof. Flower says in general terms that the canines are the last teeth to be cut, but mentions that in the gibbons they come up at the same time with, or even precede, the third molar, and this is also sometimes the case in the orang.

Giglioli says that in a chimpanzee the order is the same as in man, but that in a male gorilla he found the canines and third molar erupting simultaneously, the former teeth, however, taking the longest time to fully erupt.

The dentition of the orang approaches tolerably closely to that of man, and the points of resemblance and of difference may be fairly well seen in the accompanying figure.

The central upper incisors are similar to those of man, but are larger; the laterals are, relatively to the centrals, much smaller, and are very caniniform in shape, both inner and outer angles of their cutting edge being sloped off to such an extent that a central pointed cusp remains, in place of a thin cutting edge. The canines are strong, pointed teeth, the cingulum and the ridge joining it with the apex of the cusp being well marked upon their inner sides. In the female the upper canine is about half as long again as any of the other teeth; in the male it is longer.

The first bicuspid is a little more caniniform than that of man; its outer cusp is long and pointed, and a ridge unites it with the anterior part of the inner cusp, which is

feebly pronounced; the second is a blunter and broader tooth. The premolars are implanted by three roots. The molars are not unlike the human teeth in pattern.

In the lower jaw the incisors are large and stout; the canines sharply pointed, with a well-marked cingulum, and a well-marked median ridge on the inner side of the crown. The first premolar is a shorter, stouter, and blunter copy of the canine, and can hardly be said to have an inner cusp. In the second premolar the inner cusp is as high as the outer, and the cingulum is elevated both before and behind till it almost forms two additional cusps, but both have two distinct roots which lie anteriorly and posteriorly like those of the lower molars.

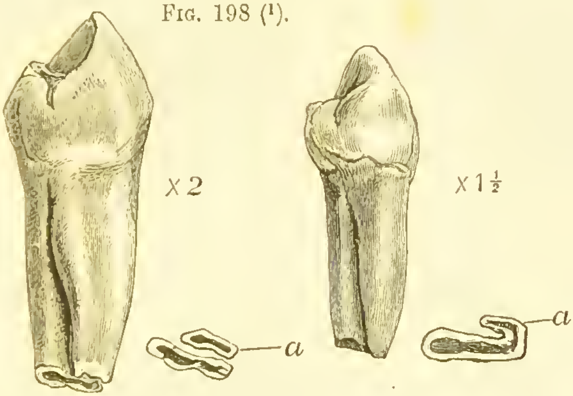
Indeed, I am not acquainted with any dentition which exemplifies the transition from incisors to canines, from canines to premolars, and from premolars to true molars, better than that of the orang.

There is also a point of interest about the lower premolars which may be noticed here. If the lower first premolar of one of the anthropoid apes be examined it will be found that its posterior root occupies the whole width of the alveolar border, but the anterior root, though when looked at from the outside it does not greatly differ, when looked at from above is found to be of much less width, and it does not extend inwards to much more than half the distance reached by the posterior root.

There is a form of abnormal root which is met with in the first lower premolar of man, of sufficient frequency of occurrence to obviously have some significance, which consists in the outer border of the root towards its apex being folded forwards and inwards, so as to present an approximation to a double root at the end. I have myself collected eighteen examples of this, and in two it has gone to the extent of a second small anterior root being completely formed.

Thus we have as a comparatively common abnormality a tendency to the formation of two roots, one anterior and the other posterior, and in every single instance it is the posterior root which is fully developed, and the anterior root is tending to be formed as a smaller root, on the outside quite level with the other, but not extending inwards in the direction of its width to nearly the same extent as the posterior root. In fact it is trying to parallel the state

FIG. 198 (1).



of things which is constant in most anthropoid apes, and is hardly explicable on any other hypothesis than that it is a reversion, for in a reduced dentition like that of a xanthocroic man it is not conceivable that there should be a tendency to the development of a second root to the first premolar as a commencement of a new order of things.

The lower molars resemble those of man, save that their surface is marked by that finely wrinkled pattern which is common to all the unworn teeth of the orang. One is struck by the great backward elongation of the jaws, by their squareness, by the parallelism of the two sides,

(1) Lower premolar (human). In the right-hand figure a second (anterior) root is in process of formation by a folding round of the flattened end of the root; in the left hand figure it has attained to being a distinct root.

which converge slightly at the back, and by the large size of the teeth in proportion to the bulk of the whole animal.

Fig. 199 ([1]).

Fig. 200 ([2]).

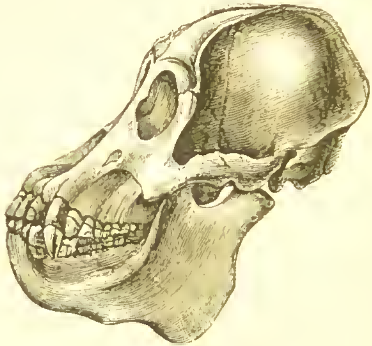
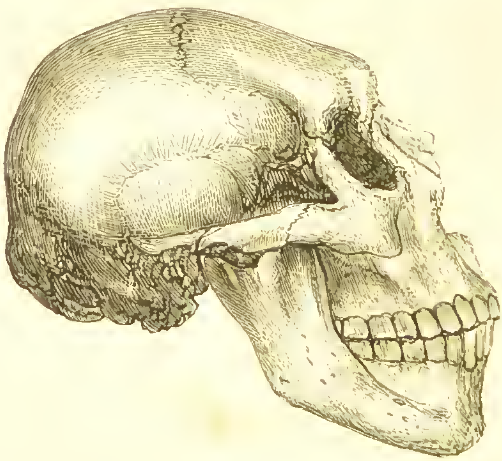


Fig. 201 ([3]).



The large size of the canines being in a measure a sexual character, is, as is so often the case, not very noticeable in the young animal; the two accompanying illustrations of

([1]) Skull of a young male Orang. The upper canine does not nearly reach to the lower alveolar border.

([2]) Skull of adult male Orang, in which the canine is largely developed.

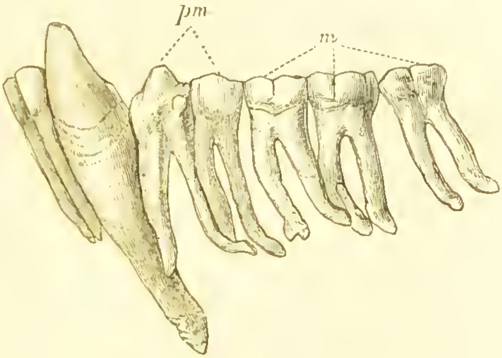
([3]) Side view of skull of an idiot.

a young and an adult male orang may serve to show this, as well as some other differences developed by age.

A peculiarity of the orang lies in the enormous length of the roots of its teeth ; this is not shared by the gorilla, the roots of whose teeth are proportionately shorter, and the chimpanzee has roots far shorter and feebler than either.

Looking at the palatine surface of the jaws of an orang,

FIG. 202 (1).



the front of the mouth is squarish, and the premolars and molars stand nearly in a straight line, not, however, strictly parallel with those of the opposite side, as they approximate at the back, the third molars being nearer together than the premolars. In the gorilla the two sides of the "arch" are parallel, and in the chimpanzee they are also nearly parallel, with a slight approximation at the back.

The teeth of the Chimpanzee are not very powerfully developed, and the third molars are a good deal smaller than the other teeth ; the lower premolars also have their two roots more or less fused.

There would appear to be a great deal of variability about the articulation of the upper and lower teeth in the higher apes. Thus in the British Museum there are three orangs

(1) Lower Teeth of Orang. Figure of jaws from which bone has been removed exposing the roots of the teeth to their ends.

which are distinctly underhung, and several whose incisors present an "edge to edge" bite. There are also three underhung chimpanzees, as well as one which is underhung in the milk dentition, a thing exceedingly rare in man. There is also an underhung gorilla, and in the museum of the Odontological Society there is a gorilla's skull in which the lower jaw contains two supernumerary teeth buried in the substance of the ascending ramus, with their crowns looking upwards, close to the foramen where the inferior dental nerve and vessels enter the bone (Odonto. Soc. Transac., vol. xix., 1887).

The differences which serve to distinguish the dentition of the most anthropomorphic apes from that of man are mainly these. Relatively to the size of the cranium, and of the whole creature, the teeth and jaws are very much larger in all their dimensions; hence the creatures are prognathous, and the facial angle small, even when compared with the jaws and cranium of an idiot. As might be expected this difference is not so great in the young as in the adult animal.

In place of the teeth being arranged in a sweeping curve, the jaws are squarish, the incisors being arranged in something approaching to a straight line between the two great outstanding canines, behind which the premolar and molar series run in straight lines, converging somewhat as they go backward. There is a "diastema" (1) or interval in front of the upper canine, into which the point of the lower canine passes, when the mouth is closed. Both the greater squareness of the jaws, and the existence of a diastema, are direct results of the great size of the canines, and are consequently not marked in young specimens.

The upper premolars are implanted by three roots, the lower by two roots, just like the true molars, and the pre-

(1) Something approaching to a diastema is said to have been observed by Vogt and Broca in early European skulls.

molars when unworn partake more of the pointed character than they do in man.

FIG. 203 [1].

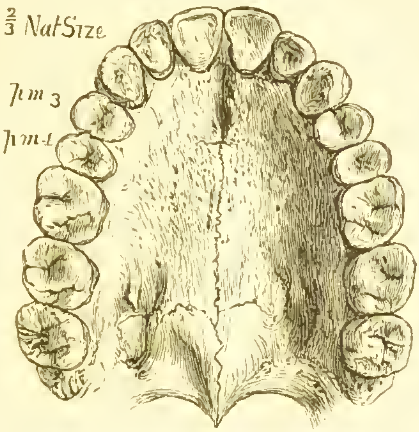
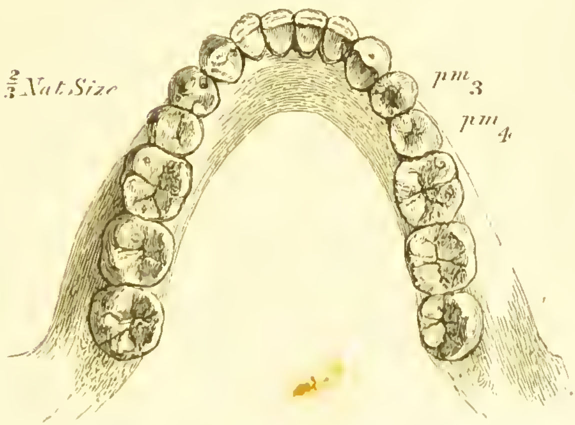


FIG. 204 [2].



The wisdom teeth present the same pattern of grinding

[1] Upper teeth of a Caffir. The oblique ridge of the upper molar is distinct, not only upon the first and second, but also upon the third molar or wisdom tooth, which in this skull has the normal three roots well marked.

[2] Lower jaw of a Caffir, in which the quinquicuspid form of the first and third molars is well seen, it being somewhat less strongly indicated in the second molars.

surface, are larger than the other molars in the gorilla and the orang, and there is abundant space for them, so that they play an important part in mastication. The molar teeth of these apes are also squarer, their cusps sharper and longer, and the characteristic patterns more strongly pronounced, than in man. Moreover the intermaxillary bone is more largely developed, and the intermaxillary suture remains distinct through life.

Anthropidæ.—In passing from the highest of the apes to the lowest of mankind, there is a sudden change in the character of the dentition; but while it cannot but be admitted that there is a gap, yet the differences are rather of degree than of kind.

Even in the lowest of human races the facial angle is greater, that is to say, they are much less "prognathous" than the apes, and the upper and lower incisors are more nearly vertical in position, not meeting one another at such an angle as in the apes. Mr. Perrin (Monthly Review Dent. Surgery, 1872) states that in a gorilla skull there is an inch of bone in front of the anterior palatine foramen: in a negro half an inch, and in a Greek skull it was close behind the incisors.

It is generally said that in man the molars decrease in size from before backwards; that is to say, that the first molar is the largest, while in anthropoid apes, with the exception of the chimpanzee, the contrary is the case. Though this is on the whole true, it requires some qualification: thus in certain lower races, such as the Australian blacks, the second and third molars are not smaller than the first.

There is no diastema; no sexual difference in dentition; no tooth projecting beyond its fellows, and the teeth are arranged in an unbroken arch. The premaxillary bones become fused with the superior maxillary early in life, whereas in the Quadrumana they remain distinct.

In general terms it may be said that the dentition of the lower races of mankind differs from that of the higher in the following particulars: the arch is not so rounded, but is squarer in front; the teeth are larger, and are disposed with greater regularity; the wisdom tooth has ample space to range with the other teeth, and is a characteristic upper or lower molar, the pattern of its grinding surface (quadricuspid if it be an upper, quinquicuspid if it be a lower tooth) and the disposition of its roots corresponding with the first and second molars, which do not greatly exceed it in size. Specimens of negro skulls may be found in which there is scanty room for the wisdom tooth, and in which consequently it is a little stunted in its development: on the other hand, plenty of well formed and well placed wisdom teeth may be picked out of European mouths, though as a rule the wisdom tooth is much smaller than the other molars, does not bear the characteristic pattern of cusps and grooves, has its roots connate, and it is not very infrequently a mere rudimentary peg. The stunted development of the wisdom tooth would seem to be a consequence of want of space during its formative period; the upper wisdom tooth is especially apt to be cramped in this way.

There is some little evidence that the wisdom tooth is in process of disappearance from the jaws of civilized races: in anthropoid apes the wisdom tooth is nearly or quite as large as the other molars, and shows no variability, whilst it comes into place almost simultaneously with the canine: in the lowest races of mankind the wisdom tooth appears to vary but little, is of large size, and is seldom misplaced; in highly civilised races it is very variable in size, form, and in the date of its appearance, is often misplaced, and is not uncommonly quite rudimentary. It seems to be a legitimate inference that a further modification of the race in the same direction will result in the disappearance of the wisdom tooth altogether.

Some exception must however be taken to such general statements: thus the Esquimaux not uncommonly have the wisdom teeth small and sometimes crowded out of place; and amongst the African races instances on the one hand of the wisdom teeth being small, and on the other, of fourth true molars existing, are to be met with.

Nevertheless, for the present, a case in which the wisdom teeth are very small can hardly be called a typical well-developed European mouth.

In many low races (Bosjesman, Negro, Australian, New Caledonian, Caffir) the second lower molar has five cusps, just like the first: this is so in the anthropoid apes, but in European races the fifth cusp is generally wanting in the second lower molar.

It is believed by Professor Cope that the quadri-tuberculate molar of European races shows a tendency to revert to a tri-tuberculate type such as is seen in Eocene lemurs.

It is not a little interesting thus to find that the differences which serve to distinguish the teeth of the lowest savage from those of a European, are to a certain extent the same with those that mark the step from a Quadrumanal to a human dentition, though of course the divergence of the dentition of the savage from that of the ape is far greater than is that of the European from the lowest savage.

It is very possible that the larger development of the jaws of the savage may be simply due to the harder work to which they are put while he is growing up. And after the attainment of adult proportions, the teeth of such a man become greatly worn down by reason of the hard and often gritty nature of his food.

It was pointed out by Mr. Mummery, in a very instructive paper ("Transactions of the Odontological Society," vol. ii., new series, 1869), that destructive wearing down of the

teeth was of very common occurrence amongst rude [1] races, while the contrary is true of highly civilised races; this was very likely due to the admixture of earth and other foreign matter with the food. And, furthermore, that the occurrence of dental irregularities, due to an insufficient size of the arches, was comparatively speaking unknown among the ruder races, whilst it has been common amongst peoples of more luxurious habits for a long period of time.

The range of variation in the size of the jaws of healthy, otherwise well-developed adults is great: thus the smallest jaw (occurring in a man of stout build, above middle height) with which I am acquainted measures in width only $1\frac{1}{2}$ inch, and in length from back to front $1\frac{3}{4}$ inch; while the largest (occurring in a gentleman of lesser stature; of Basque extraction, moreover, which makes it the more striking) [2] measures no less than $2\frac{1}{2}$ inches in width and $2\frac{1}{4}$ inches in length: and even larger dimensions are recorded in the "Dental Cosmos" of September, 1876; the width being taken between the centre of the alveolar borders at the position of the wisdom teeth, and the length being measured on a line drawn from the incisors to another line joining the two wisdom teeth.

On the whole, it must be said that there are fewer constant differences between the teeth of the various races of mankind than might have been *à priori* expected; in fact, we may almost say that the teeth of savage man are pretty much what we should look upon as an exceedingly perfectly formed set of teeth if we were to see them in the mouth of a European.

Prof. Flower (Journ. Anthropol. Instit., March, 1885),

(1) To those races mentioned by Mr. Mummery may be added the mound-builders of North America, whose teeth were always worn down to an excessive extent.

(2) Magitot (Bullet. de la Soc. Anthropol. de Paris, 1869) says :—"Les Basques, par exemple, remarquables par la petitesse extrême de leursdents."

has investigated the relation of the size of the teeth to that of the skull very closely, with the result of bringing out certain race distinctions. As measures for comparison he takes the length of the cranio-facial axis, measured from the front edge of the occipital foramen to the naso-frontal suture, and the length from the front of the first premolar to the back of the third molar *in situ*. His "Dental Index" is arrived at thus

$$\text{Dental Index} = \frac{\text{Length of Teeth} \times 100}{\text{Cranio-facial axis}}.$$

This gives figures ranging from 42 (microdont), 43 (mesodont), 44 and upwards (megadont).

As in the female the skull is smaller whilst the teeth are the same, a slightly higher index is arrived at in them:

The Microdont races are—

European.	Egyptian.
British.	Polynesian.

The Mesodont are—

Chinese.	Malays.
American Indian.	Negroes.

And the Megadont—

Melanesians.	Australian.
Andamanese.	Tasmanian.

As to this classification it is to be remarked that the teeth of Polynesians are actually larger than those of Europeans, but the cranio-facial axis is of extreme length, so that the index is reduced; this is also the case with the American Indians, whilst the Andamanese are brought into the Megadont series by the relative size of teeth to the basis cranii, though in this small people the teeth are actually small.

The dental index of Megadont races being from 44–47, that of the chimpanzee is little more than the highest of

these, namely 47·9, whilst the orang rises to 55, and the gorilla to 54, but in the gibbon the index is as low as 41·7. It is, however, the opinion of the African traveller Mr. Stanley, that the teeth of African races vary in accordance with the build of the individual, and particularly with the size of the jaws, such small races as the Somalis having small teeth. It does not appear, however, that these impressions are based upon actual exact measurement, but only upon general appearance. He mentions that many of the races who show no regard for cleanliness otherwise, assiduously clean their teeth.

The dental formula of man is of course

$$i\ \frac{2}{2}\ c\ \frac{1}{1}\ p\ \frac{2}{2}\ m\ \frac{3}{3}.$$

But the question has recently been raised as to which of the incisors of the typical mammalian dentition are wanting.

Prof. Sir W. Turner ("Journ. Anat. and Physiol.," 1885), and Mr. Andrew Wilson ("British Denl. Assoc. Journ.," 1885), bring forward a certain amount of evidence which raises a doubt as to whether it is not i_2 which is missing in man. In cases of cleft palate the cleft is often demonstrably not in the line of the intermaxillary suture but well within it, and there is often an incisor-like tooth on the canine side of the cleft as well as two on the other side of it, a so-called "precanine." The frequency of occurrence of this tooth, and a study of those cases in which the incisors are present, lend some support to the idea that it is i_2 which is lost in the ordinary human dentition.

CHAPTER XI.

THE TEETH OF MARSUPIALIA.

The great sub-class of Marsupials, consisting of animals very sharply marked off from placental Mammals by many striking peculiarities, and amongst others, by the very helpless condition in which the fœtus is born, was once very widely distributed over the globe. Now, however, Marsupials are numerous only in Australia, where they are almost the sole representatives of the Mammalian class; there are a few Marsupials elsewhere, as in America (Opossums) and New Guinea; but there are no Marsupials in Europe, most parts of Asia, and Africa.

The Marsupials of America are all Opossums (*Didelphidæ*), and this family is not represented in Australia. There is evidence to indicate that the Marsupials of America have nothing at all to do with the Australian Marsupials, but were derived from a different source, at the time when Marsupials abounded all over Europe.

The Marsupials of Australia almost monopolise that country: thus Mr. Wallace says of it: "The Australian region is broadly distinguished from all the rest of the globe by the entire absence of all the orders of non-aquatic mammalia that abound in the old world, except two—the Winged Bats (*Chiroptera*), and the equally cosmopolitan Rodents. Of these latter, however, only one family is represented—the Muridæ—(comprising the Rats and Mice), and the Australian representatives of these are all of small or moderate size—a suggestive fact in appreciating the true character of the Australian fauna.

"In place of the Quadrumana, Carnivora, and Ungulates, which abound in endless variety in all the other zoological regions under equally favourable conditions, Australia possesses two new orders or sub-classes, Marsupialia and Monotremata, found nowhere else in the globe, except a single family of the former in America.

"The Marsupials are wonderfully developed in Australia, where they exist in the most diversified forms, adapted to different modes of life. Some are carnivorous, some herbivorous, some arboreal, others terrestrial. There are insect-eaters, root-gnawers, fruit-eaters, honey-eaters, leaf or grass-feeders.

"Some resemble wolves, others marmots, weasels, squirrels, flying squirrels, dormice, or jerboas.

"They are classed in six distinct families, comprising about thirty genera, and subserve most of the purposes in the economy of nature fulfilled in other parts of the world by very different groups; yet they all possess the common peculiarities of structure and habits which show that they are members of one stock, and have no real affinity with the old-world forms, which they often outwardly resemble."—"Geographical Distribution of Animals," p. 391.

I have quoted this passage from Mr. Wallace, because much of it is applicable to the teeth.

In Australia, the present home of the marsupials, representative species abound; that is to say, widely different though the animals really are, there are many genera and species which have the habits of, and, as it were, fill the place of such creatures as the Carnivora and Insectivora and Rodents amongst the placental mammalia. And not only do they possess something of their habits and external configuration, but in those characteristic structures which are subservient to the creature's immediate wants, the marsupial representatives closely mimic the more highly organised placental mammals. Thus the teeth of an insect-eating marsupial very closely resemble those of a true Insectivore, though retaining certain eminently marsupial characters; in the same way the dentition of the marsupial Thylacine mimics that of a dog (compare Figs. 206 and 207).

And although marsupial dentitions do vary very much, yet there are many transitional forms by which we are sometimes able to trace the successive modifications through which extreme divergence has been ultimately attained.

Just as we ascribe to placental mammals the formula—

$$i\,\frac{3}{3}\;c\,\frac{1}{1}\;p\,\frac{4}{4}\;m\,\frac{3}{3}=44$$

as the typical or parent dental formula, so recent marsupials possess the following—

$$i\,\frac{3}{3}\;c\,\frac{1}{1}\;p\,\frac{3}{3}\;m\,\frac{4}{4}=44.$$

Though no living marsupial has more than three premolars, it may be presumed that four was the original number, as in placental mammals, and Mr. Oldfield Thomas has found in Dasyurus and in Phaseologale dorsalis a fourth tooth, in the position of pm_2; he infers, therefore, that it is pm_2 which has been lost by recent marsupials, and further points out that a marked gap exists in this situation in Didelphys, Perameles, and others. In several of the earlier fossil marsupials, *e.g.*, Triconodon, Ctenacodon, Plagiaulax, and others, there are four premolars and four true molars.

The marsupials are grouped into :—

(i.) Teeth with definite roots.

(*a.*) Diprotodonts, i $\frac{3}{1}$. The central, upper, and the lower incisors, are large and trenchant, the canines small or absent: *e.g.*, Macropus and Phalangista.

(*b.*) Polyprotodont.—Teeth rooted, incisors numerous, small and subequal; canines large, and molars strongly tuberculated: *e.g.*, Didelphys.

(ii.) Teeth all of persistent growth: *e.g.*, Phaseolomys (Wombat).

Though the total number of teeth is the same as in placental mammals, the marsupial has only three premolars and has four true molars. The premolars (false molars) differ from the true molars in the greater simplicity of their crowns, just as in most placental mammals; but, although, looking at the complete adult dentitions, no hesitation would be felt in classing the teeth under the heads of premolars and true molars, yet there is a curious anomaly in the succession of the teeth which applies to the whole of the subclass Marsupialia, and to some extent invalidates the definition of "premolar" as applied to their teeth. Only one of

the premolars (the hindmost) has vertically displaced a milk tooth; indeed, the whole milk dentition of marsupials consists of four milk molars (one on each side of each jaw), there being no milk incisors nor canines in any known marsupial. It is further pointed out by Professor Flower, who was the first to fully describe these peculiarities in the succession of marsupial teeth ("Phil. Trans.," 1867), that the extent to which the solitary milk molar is developed varies much in the different families; no trace of any succession has been observed in the Wombat; in the Thylacine (a dog-like creature) the small milk molar is calcified, but is absorbed or shed prior to any other teeth being erupted; whilst in the Kangaroos it is retained till a much later period (see page 478), and in the Kangaroo Rat (Hypsiprymnus) the milk molar has not yet given place to its successor at the time when the last permanent molar has come into place, so that it for a long time ranges with the other teeth and does work.

This subject has been further investigated by Mr. Oldfield Thomas, who has found that the Dasyuridæ present the same milk dentition as the other families, that is to say, that some have a well-developed milk molar, and that it occurs in various phases of reduction, some having none at all ("Phil. Trans.," 1887). This author writing of Phascologale, one of the Dasyuridæ, says:—

"The normal state of a member of this group is to have three well-developed premolars, the last one of which has a milk predecessor. Then a tooth reduction has taken place, all of which has fallen upon what is evidently a peculiarly plastic tooth, *i.e.*, pm_4, and this, with the milk tooth preceding it, has been decreased in various degrees and in the end suppressed, as in the allied genera Dasyurus and Sarcophilus."

Those species which have a large pm_4 have preceding it a tricuspid milk tooth, but as pm_4 gets reduced, the milk

tooth preceding it is reduced still faster till it quite aborts : even then the pm_4 presents the peculiarity of being erupted, and indeed not being calcified, until later than the other teeth.

The question whether the tooth change of the marsupials is the remnant of a more complete change in an ancestral form, or is the dawning of a more complete change, is discussed at length by Mr. Oldfield Thomas.

That it is the first formation of a change he holds strongly, mainly because the marsupials are at a lower stage of evolution, and so it would be unlikely that they had once evolved a change, and then evolved it away again, seeing that is clearly useful to placental mammals—because five out of the six marsupial families have precisely the same amount of tooth change, which would be unlikely if it were an atavism—and, because no fossil marsupials present any indication of a fuller change, but have just the same.

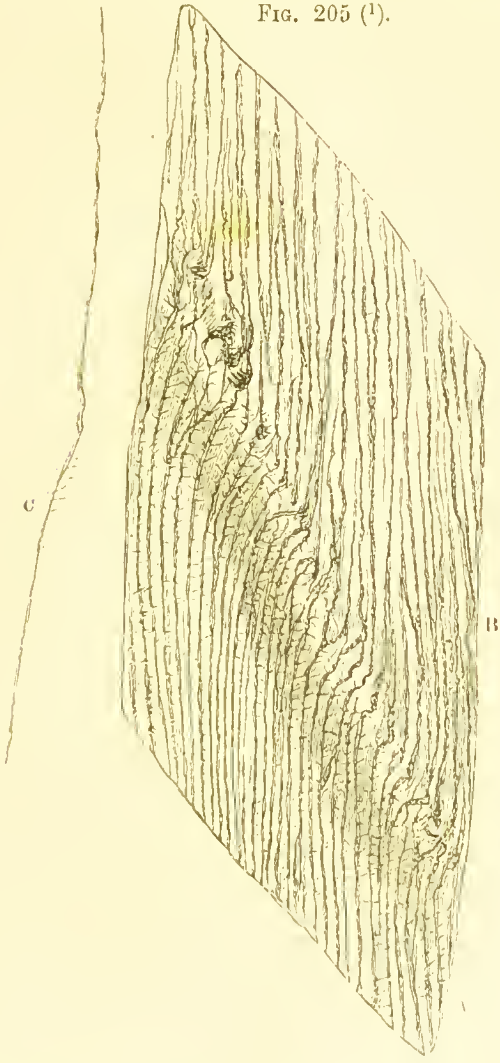
This peculiarity of the possession of a single milk tooth was fully established even in Mesozoic times, as is exemplified in Triacanthodon and other Mesozoic marsupials.

Mr. Oldfield Thomas suggests as an explanation, that there first took place a retardation of a back permanent tooth, perhaps useful for "packing" purposes in a jaw as yet small, and that when the retardation had gone to a certain point, a milk tooth was developed to fill the gap in the series which would otherwise have existed.

It is difficult to obtain very young marsupials, and material for the complete elucidation of the subject is wanting ; but I have had the opportunity of making sections of the jaws of several young specimens (Perameles and Halmaturus), taken from the pouch by my friend Prof. Moseley, and I have not so far succeeded in finding any uncalcified germs or other indications of any more teeth of a milk dentition.

A further peculiarity of the marsupials is the structure of

FIG. 205 [1].



[1] Enamel and dentine of a Kangaroo (Macropus major).
The dentinal tubes in the dentine (A) are furnished with numerous short branches at the line of juncture with the enamel ; they are dilated, and a little bent out of their course, while beyond the dilatation they pass on through about two-thirds of the thickness of the enamel in a straight course and without branches. Only a part of the whole thickness of the enamel is shown in the figure. B. Enamel penetrated by the tubes. C. Individual dentinal tube.

their enamel, which is penetrated by the dentinal tubes. My father, some years ago, described and figured the teeth of a large number of marsupial genera ("Phil. Trans.," 1850), and found that although in the different families the tube system of the enamel varied in its richness and in the depth to which the tubes penetrated, yet it was conspicuously present in the whole class, with the sole exception of the Wombats, in whom nothing of the kind is to be found. Prof. Moseley's specimens have afforded to me the opportunity of studying the development of this tubular enamel, and the result of my investigations will be detailed elsewhere; but it may be mentioned that the formation of the enamel tube appears to be precisely analogous to that of a dentine tube, and at a certain period the enamel cells have appended to them long processes like the dentinal fibres. The dilatation noticeable at the boundary line of the enamel and the dentine (see Fig. 205) is a kind of clumsy joint brought about by the coalescence at this point of the tube-forming cells—on the one side odontoblasts, on the other enamel cells.

There exists one genus of flesh-eating marsupials whose ferocity is such as to have gained for them the names of wolf and tiger, while the resemblance of the head to that of a dog has given origin to the popular name of "dog-headed opossums" (1).

The resemblance to the dog in dentition is even more close than in external form: whilst retaining certain marsupial attributes, the teeth of the Thylacine are, so far as their working capabilities go, almost exactly like those of the dog. The dental formula is—

$$i\ \frac{4}{3}\ c\ \frac{1}{1}\ p\ \frac{3}{3}\ m\ \frac{4}{4}.$$

The incisors are small, close set, and sharp edged, the

(1) It has of course no real relationship to the true opossums, which are not found in Australia.

outermost being somewhat caniniform. The canines are stout, pointed teeth, not quite so long relatively as those of a dog. The premolars are conical teeth, implanted by

FIG. 206 (1).

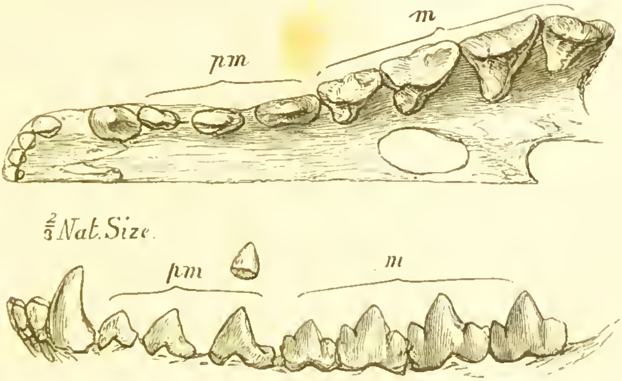
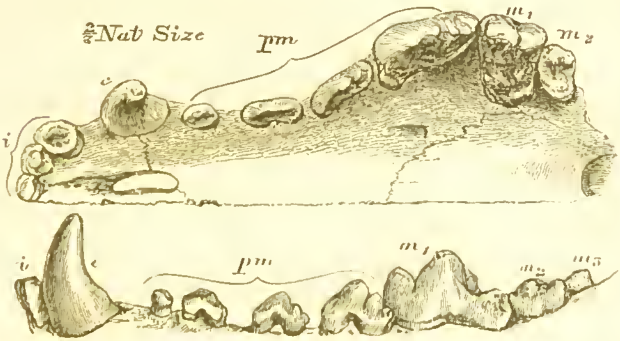


FIG. 207 (2).



two roots, and very similar to those of the dog; they are followed in the upper jaw by four molars, increasing in size

(1) Upper and lower teeth of the Thylacine. The rudimentary milk molar, which is absorbed before birth, has been placed over the third or last of the premolars, which succeeds to it vertically.

(2) Upper and lower teeth of a Dog, which are placed side by side with those of the Thylacine, to show the many points of resemblance between the two dentitions.

from the first to the third, but the last true molar is again a smaller tooth.

The upper molars are all of the "carnassial" pattern; there is a "blade" elevated into subsidiary cusps, and internally to this a "tubercle," supported by a third root.

The lower molars also bear some resemblance to the carnassial teeth of the dog, consisting of a strong, sharp-edged blade, with anterior and posterior subsidiary cusps, the latter being somewhat broad and tubercular.

An allied animal (Dasyurus ursinus), though smaller than the Thylacine, and having teeth of a less sectorial character, is so destructive to sheep and so fierce and untamable, that it has earned the name of "Tasmanian Devil."

Within the limits of the same genus, a species (Dasyurus viverrinus) is to be found, in which the molar teeth are studded over with long sharp cusps, like the teeth of Insectivora, a group which it resembles both in its habits and food.

A number of smaller marsupials approximate in their dentition more or less to the Insectivorous type, whilst a tolerably complete chain of existing forms serves to bridge over the gap between the rapacious Dasyuridæ and the herbivorous Kangaroos and Wombats.

Amongst the Opossums the larger species have large canines, and a dentition in its general features approximating to the Dasyuridæ; they feed upon birds and small mammals, as well as upon reptiles and insects, while the smaller species are more purely insectivorous.

Myrmecobius, a small Australian marsupial of insectivorous habits and dentition, is remarkable as having teeth in excess of the number of the typical mammalian dentition, having—

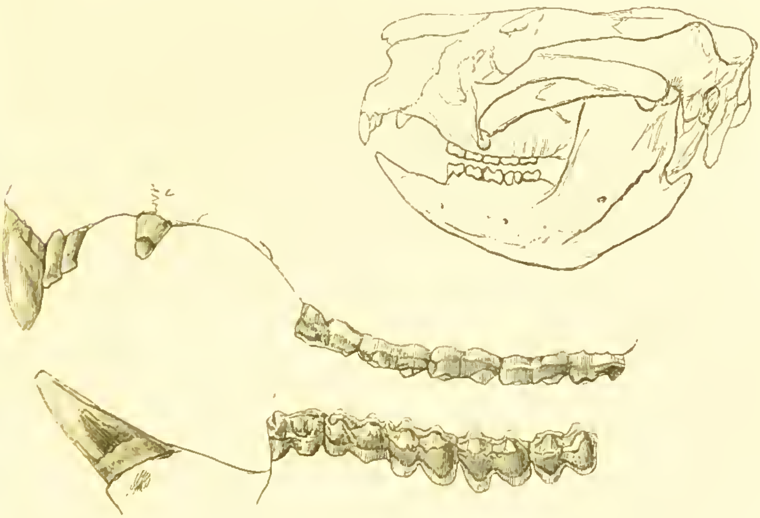
$$i\,\frac{4}{3}\;c\,\frac{1}{1}\;p\,\frac{3}{3}\;m\,\frac{6}{6}.$$

In the Phalangers, nocturnal arboreal animals found in

Australia and a part of the Malay Archipelago, the canines, though present, are feeble; an interspace also separates the incisors from the molar series.

The lower incisors, reduced to a single pair, are procumbent, and grow from persistent pulps; there is thus functionally some faint approach to the character of a rodent

Fig. 208 (1).



dentition, as may be seen by an inspection of the accompanying figure, though there is a strongly marked transverse condyle to the lower jaw. Phascolarctos cinereus has been shown by Mr. Oldfield Thomas to have the same reduced milk dentition as Thylacinus.

The name "Kangaroo Rats" (Hypsiprymnus) is applied to a genus consisting of about a dozen species; they are all small creatures, not much larger than rabbits, but having the general proportions of Kangaroos. They are quiet,

(1) Teeth of Phascolarctos cinereus. An outline figure of the skull is placed above to show the general "rodent" aspect of the skull.

gentle little creatures, of strictly herbivorous habits, and they are interesting to the odontologist as possessing a dentition which throws some light upon several anomalous extinct forms, whose habits and affinities have been the subject of much controversy.

The dental formula is—

$$i\,\frac{3}{1}\;c\,\frac{1}{0}\;p\,\frac{1}{1}\;m\,\frac{4}{4}.$$

The first pair of upper incisors are sharply pointed, are directed nearly vertically downwards, and grow from persistent pulps. The second and third do not grow from persistent pulps, and their worn crowns do not attain to the same level as those of the first pair.

All three pairs are antagonised by the single pair of large procumbent lower incisors, of which the sharp points meet the first pair of upper incisors, while the obliquely-worn surface behind the cutting edges impinges against the second and third upper incisors.

The arrangement of the incisors, and the sharpness of their cutting edges, are calculated to effect the same objects as those attained by the incisors of a rodent: a still closer resemblance would be brought about by the dwindling (which occurs in other genera) and final disappearance of the second and third upper incisors, and a compensating extra development of the first pair.

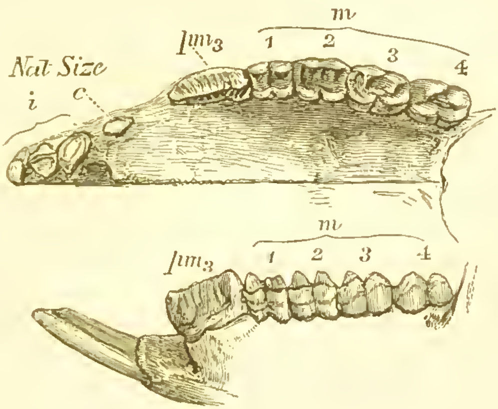
The canines are not large; yet they are not so small as to be termed rudimentary; in the lower jaw they are absent.

Only one premolar exists in the adult, and this is a very peculiar tooth; its crown is very long from back to front (at least twice as long as any of the molars, and in some species as long as three of the molars), and consists of a finely furrowed blade with a sharp edge; the blades of the upper and lower teeth slide over one another. Behind this

there are four true molars, with square quadricuspid crowns, which become much worn down by use.

The last and only premolar, the tooth to which attention has already been drawn on account of its size and other peculiarities, by virtue of its great size displaces not only the

FIG. 209 ([1]).



milk molar, to which it is the legitimate successor, but also turns out the premolar in front of it, a tooth belonging to the "permanent" series.

In this particular the succession of the teeth in the Hypsiprymnus is the same as that of the true Kangaroo, which may be understood by a reference to Fig. 211.

There are some extinct marsupials, known only by their jaws, which have been the subject of much controversy. Professor Owen, basing his arguments largely upon the presence of premolars which possessed elongated and sharp-edged blades, held that *Plagiaulax* and *Thylacoleo* were carnivorous, saying of the latter that it possessed the simplest and most effective dental machinery for predatory life known

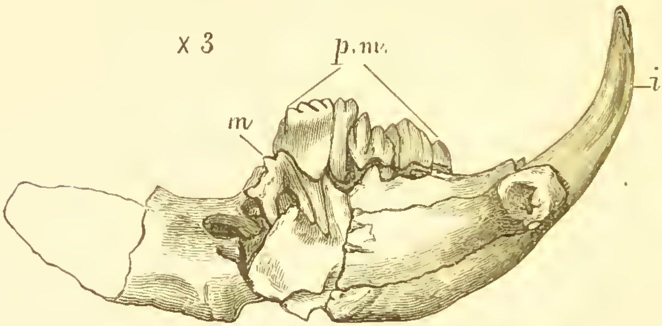
([1]) Upper and lower teeth of Hypsiprymnus (Bettongia) (Graii ?). The dentition represented is that of the adult animal, the permanent premolar (pm_3 in the figure, pm_4 if we accept Mr. Oldfield Thomas's views—cf. p. 466) being already in place.

among mammalia; Dr. Falconer, in the case of the first, and Professor Flower in the case of the Thylacoleo, having shown this view to be untenable, or at least unsupported by adequate evidence.

Prof. Marsh has described several Mesozoic forms like Plagiaulax, but upper and lower jaws not having been found together *in situ* it is somewhat problematical which upper belongs to which lower jaw.

The lower jaw of Ctenacodon, found in strata of Jurassic

Fig. 210 ([1]).



age, has a single long pointed incisor, four compressed cutting premolars, and two minute tubercular molars behind them.

The clue to the nature of the great blade-shaped teeth of these extinct creatures is afforded by the form of the premolar of the herbivorous Hypsiprymnus (see Fig. 209). The incisors were reduced in number, and were large; the teeth between them and the large premolar were stunted; but both these points are true of the herbivorous Kangaroos. The Thylacoleo differs, however, from all known animals by the immense size of the thin-edged premolar (worn flat in aged animals), and by the rudimentary condition of its true molars. But its incisors, lying forwards and closely ap-

([1]) Lower jaw of Ctenacodon (after Marsh).

proximated in the middle line, are particularly unsuitable for catching and holding anything alive and struggling, whilst the nearest resemblance to the blade-shaped tooth is to be found in harmless herbivorous creatures, so that the balance of evidence is much against Professor Owen's view.

The dental formula of Thylacoleo was—

$$i\ \frac{3}{1}\ c\ \frac{1}{0}\ p\ \frac{3}{1}\ m\ \frac{1}{2}.$$

The first upper incisor was very large, and the second and third very small, as were the canine and the first two upper premolars; but the last upper and the only lower premolars were great blade-shaped teeth like the large premolar of Hypsiprymnus, only far larger.

Thus its useful teeth were only a pair of incisors above and below, and a pair of sectorial premolars.

The Kangaroos, comprising many species of very varying size, are all docile creatures (with the exception of a few old males), of herbivorous habits; they in some particulars recall the ruminants.

Their dental formula is—

$$i\ \frac{3}{1}\ c\ \frac{0}{0}\ p\ \frac{1}{1}\ m\ \frac{4}{4}.$$

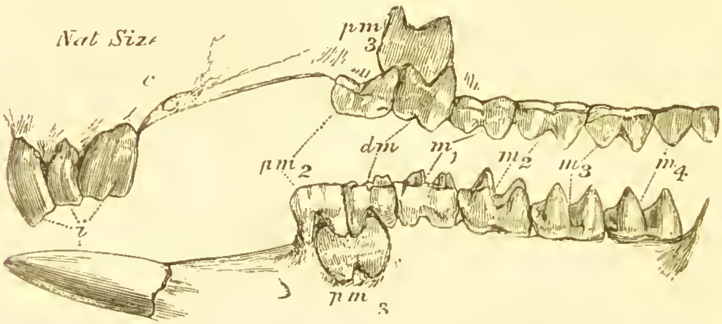
The three pairs of upper incisors are more equal in size than in the Hypsiprymnus, and the central pair do not grow from persistent pulps. The lower incisors are very peculiar teeth: they grow from persistent pulps, are procumbent, projecting forwards almost horizontally, and are very much flattened from side to side, their outer surfaces being but slightly convex, and their inner surfaces flat, with a median ridge. Their margins are almost sharp. There is an unusual amount of mobility between the two halves of the lower jaw, so that these two teeth can be to a slight extent separated from one another.

The upper canine is often present as a very minute

rudiment, but in no Kangaroo does it attain to a greater size.

The dentition of the Kangaroo is somewhat perplexing to the student, for two reasons: the one, that the last or third permanent premolar not only displaces the solitary milk molar, but also, as in Hypsiprymnus, on account of its

Fig. 211 (1).



greater size, the second permanent premolar, which was in front of the milk molar; and, besides this, in animals past adult age, teeth are shed off from the front of the molar series till at last only the last two true molars on each side remain.

Thus the dentition of the Kangaroo at successive ages may be thus represented—

$$\text{i}\ \frac{3}{1}\ \text{c}\ \frac{0}{0}\ \text{p}\ \frac{1}{1}\ \text{dm}\ \frac{1}{1}\ \text{m}\ \frac{4}{4},$$

or, in all, six molar teeth. Then the third premolar displaces

(1) Upper and lower teeth of Halmaturus ualabatus. The permanent premolar is not yet erupted, and is shown in its crypt: when it comes into its place it will displace the milk molar, and one of the anterior premolars as well. In the upper jaw a rudimentary canine is shown. The point of the lower incisor would fit, in closure of the mouth, behind the long anterior upper incisor, but the width of the page did not admit of the teeth being placed in their true relative positions without reduction in size.

the second true permanent premolar as well as the milk molar, and we have—

$$i\,\frac{3}{1}\;c\,\frac{0}{0}\;p\,\frac{1}{1}\;\text{(a new one)}\;m\,\frac{4}{4},$$

or, in all, only five molar teeth.

Then, one after another, teeth are shed off from the front of the molar series, just as in the Phacochærus (see page 406), till all that is left is—

$$i\,\frac{3}{1}\;c\,\frac{0}{0}\;p\,\frac{0}{0}\;m\,\frac{2}{2}.$$

The milk molar of the Kangaroo is a fully-developed tooth, which takes its place with the other teeth, and is not distinguished from them by any special characters, so that mere inspection of the jaw of a young Kangaroo having it in place, at the same time with a premolar in front of it and four true molars behind it, would not lead an observer to suspect its real nature.

No existing creature serves to connect the Kangaroos closely with the Wombat, but the extinct Diprotodon appears to have in a measure bridged across the gap.

The Wombats (Phascolomys) are heavily-built, inoffensive creatures, which burrow in the ground and subsist largely upon roots. In their dentition they closely simulate the rodents, as they possess but a single pair of chisel-edged incisors in either jaw, growing from persistent pulps, and embedded in very deep and curved sockets. These differ from the corresponding "dentes scalprarii" of true rodents in that there is a complete investment of cement, which passes over the enamel in front of the tooth as well as covering its back and sides. They are unlike the teeth of other marsupials in their structure, as the dentinal tubes do not penetrate the enamel, which is therefore, probably, harder and denser and so less readily worn away.

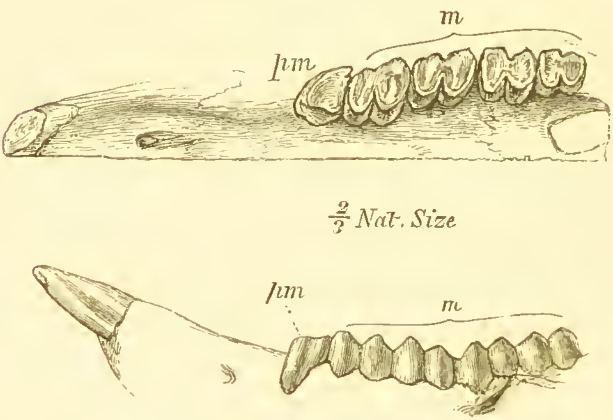
The molar teeth also grow from persistent pulps, and are very deeply grooved upon their sides, so that their grinding surfaces are uneven.

Their dental formula is—

$$i\ \frac{1}{1}\ c\ \frac{0}{0}\ p\ \frac{1}{1}\ m\ \frac{4}{4}.$$

The first tooth of the molar series is a single column,

Fig. 212 ([1]).



whereas the deep grooving of the others divides them into two columns, so that its simpler appearance, as well as analogy, would indicate that it is a premolar. But no succession whatever has been observed in the Wombats.

The adaptive resemblance to the dentition of the true rodents is exceedingly close, though the Wombat is an undoubted marsupial; and the very closeness of the imitation is an exemplification of the fact that adaptive characters are very apt to mislead, if used for the purposes of classification.

Extinct Wombats, of very much larger size than the

([1]) Upper and lower teeth of Wombat (Phascolomys wombat).

recent species, are found in the later tertiary deposits of Australia.

Amongst the marsupials there is a pretty little arboreal creature (Tarsipes), not larger than a small rat, which subsists upon insects and the nectar of flowers, which it reaches by means of a long protrusible tongue. Its molar teeth are rudimentary, variable in number, and are soon shed; the lower incisors, which are procumbent, are however retained, as are a few small teeth which are opposed to them above.

The wonderful diversity of the forms into which the marsupials have branched out in Australia seems to prove that they have been established in that region, and have been without the competition of more highly organised placental mammals, for a prodigious length of time; and one cannot better conclude the very brief survey of the teeth of mammalia which has been attempted in this volume than by calling the reader's attention again to the character of the marsupial fauna—this microcosm, in which every place is filled by a marsupial which mimics the placental mammal which it represents—for nowhere can we more plainly see the workings of natural selection than in areas thus isolated and deprived of immigrant creatures for countless ages.

In the foregoing pages much stress has been laid upon the variability of animals, and the agencies by means of which the variations have been preserved and intensified, so to speak, so that ultimately permanent hereditary modifications have been the result, variations be it noted not always small (see p. 294); and it is possible that in laying this aspect of the matter prominently before the reader an impression of too great instability may have been conveyed; and thus the teeth of creatures made to appear more plastic and more shifting than they really are, for it is hardly possible to realize the enormous lengths of time

during which the agencies have been at work, and without which they would have been powerless to produce profound alterations.

The process which we term inheritance is constantly reproducing animals which are minute copies of their parents; copies which are even more exact than we can at first sight realise.

Thus, even amongst different species of the same genus, whose teeth are apparently quite similar so far as their number and pattern goes, differences exist which are constant for the species, and which may be brought into prominence by any method of investigation which is sufficiently accurate. And those engaged in the practice of dental surgery meet with curious examples of inherited variation, sometimes taking the form of irregularity in the position of teeth, and sometimes of the absence or dwarfing of a particular tooth; these abnormalities, running through several generations, are often presented by a large proportion of the children of one generation.

Nature is never extravagant, and an organ which owing to altering conditions is becoming superfluous, is sure to be destroyed. For the operation of natural selection is just as necessary for the preservation of an organ which has arrived at a certain standard by the process of evolution as it was for the bringing it up to that standard—the remission of the operations of natural selection lead surely to its degradation and final disappearance.

And so it happens that whilst an organism is as a whole progressing, some of its parts may be becoming superfluous, and be retrograding, after a time coming down to the condition of rudimentary organs. Thus almost all early mammalia had a continuous row of teeth, with no diastema; from this the teeth of monkeys had advanced in specialisation and acquired a diastema, but in man the diastema has been lost again, so that quâ the teeth, man has retrograded.

It is perhaps disappointing that, comparatively simple, accessible and indestructible as teeth are, no satisfactory comprehensive scheme of their evolution even in mammalia has been set forth. The extreme imperfection of the geological record is such that, with the exception of a few comparatively small groups, the material upon which to build wide generalisations is not to hand, and too many gaps remain to be bridged over by conjecture.

Professor Cope, who is an advocate of the mechanical genesis of tooth forms, has been the chief worker in this field (Homologies and origin of types of molar teeth, Journ. Philadelph. Acad. 1874, and numerous papers in American Naturalist), and he holds that the primitive mammalian tooth must have been a simple cone, like a cetacean tooth ("Haplodont"), and that this was first complicated by the addition of low cusps before and behind, and subsequently also laterally.

These early teeth would have alternated with one another in closure of the jaws, and this alternation of the teeth lasted for a long period in geologic time.

It has been pretty well established by Professor Cope and Professor Osborn (p. 318) that Mesozoic mammals had attained the stage in which the molars were trituberculate, but the teeth still interdigitated, and did not meet grinding surface to grinding surface.

But although Professor Cope's researches have been of the utmost value, and some of his terms have obtained general currency, fresh facts are continually coming to light, which render attempts at absolute generalisation almost futile. As an example we may take the recently discovered teeth of Ornithorhyncus. Now this is a mammal of so low a type, and with so many affinities with the Sauropsida that we might have fairly expected that, if it had teeth at all, they would have been of the simplest conical form. But instead of their being such, they are of complex form, and show

indications of descent from some creature in which they were more complete, and functionally more active.

So this discovery, instead of helping us much in our speculations, seems to relegate to a still more remote period that common ancestor whose teeth were all simple cones, if such there were; but there remains an ample scope for work of this kind in the study of the homologies of the teeth of those ancient animals which are already known, whose numbers are being added to almost every day.

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